QUANTITATIVE ESTIMATION OF RATES OF ARTHROPOD PREDATION ON VELVETBEAN CATERPILLAR (*Anticarsia gemmatalis* Hübner) EGGS AND LARVAE IN SOYBEANS

BY

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"'Would you tell me, please, which way I ought to go from here ?'
'That depends a good deal on where you want to get to,' said the Cat.
'I don't much care where -' said Alice.
'Then it doesn't matter which way you go,' said the Cat."

Lewis Carroll 1865
Alice's Adventures in Wonderland

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A method is presented for quantitative estimation of rates of arthropod predation on velvetbean caterpillar, Anticarsia gemmatalis Hübner (Lepidoptera: Noctuidae), eggs and larvae under field conditions. The method used the combination of mark-release-recapture of prey and direct observation techniques to partition estimates of total mortality into predator-induced and non-predator-induced components. The predator-induced component could be further partitioned according to predator species.

The method was tested in 1980 by using it to estimate rates of arthropod predation on small and medium velvetbean caterpillar (VBC) larvae. The results from this test suggested the refinements necessary to improve the utility of the method. These refinements

were incorporated into the method that was used to estimate rates of predation on VBC eggs and larvae and small larvae in 1981 and 1982.

The mean daily rates of predation averaged over the season (number of seasons considered in calculation of the mean) were estimated to be 24% for eggs (1), 25% for small larvae (3), 23% for medium larvae (2), and 35% for large larvae (1) at prey densities ranging from 6-20 immatures per 91 row-cm. The predator species responsible for this mortality varied with life stage, field, and year.

The impact of the arthropod predator complex on VBC population dynamics was assessed by examining patterns of predator-induced mortality and the response of the predator complex to changes in prey and predator population densities. The predator complexes present in 1980-1982 appeared to inflict a constant level of daily mortality on VBC immatures throughout the season. The response of the predator complex present each year to changes in prey and predator population densities appeared to be overridden by changes in leaf area. To understand more completely the influence of leaf area will require further study.

The proposed method for quantifying arthropod predation has utility in estimating rates of arthropod predation on immature life stages of a single noctuid pest or a complex or noctuid pests in row crops. The need for such estimates in understanding the role of arthropod predators in pest population dynamics is discussed.

INTRODUCTION

Prediction of pest population dynamics is paramount in the development and evaluation of pest management programs. Such prediction, however, presupposes an understanding of the impact of mortality agents on pest population dynamics. One of the major mortality agents influencing pest population dynamics in agricultural systems is arthropod predators (Whitcomb 1973). Understanding their role facilitates prediction of both the time of occurrence of economically injurious levels of pest populations (Barfield and Stimac 1980) and the expected amount of mortality imposed on a pest population by arthropod predators (Huffaker et al. 1971). Prediction of both quantities aids in the consideration of the consequences of the use of various pest suppression tactics, prior to their inclusion in a pest management program. Prediction of the impact of arthropod predators on pest population dynamics assumes that rates of arthropod predation may be estimated quantitatively.

In the development and evaluation of pest management programs for Florida soybeans, the population dynamics of the major defoliating pest, the velvetbean caterpillar, Anticarsia gemmatalis Hübner (Lepidoptera: Noctuidae), must be predicted. This requires an understanding of the role of arthropod predators in velvetbean

caterpillar (VBC) population dynamics because previous studies of predation on VBC eggs (Buschman et al. 1977a) and of the effects of insecticides on VBC population dynamics (Shepard et al. 1977, Brown and Goyer 1982) have demonstrated that arthropod predators can impose significant mortality on VBC life stages. Unfortunately, these studies have not provided quantitative estimates of predation that are necessary for the construction of dynamic multipredator-prey models. Such models are required in the prediction of VBC population dynamics over a wide geographic area, such as north central Florida, because in Florida soybeans there are approximately 120 species of potential VBC predators (Whitcomb, unpublished data)[1] whose densities vary over space and time. The initial step in the construction of a multipredator-prey model is the partitioning of estimates of pest mortality into predator-induced and non-predator-induced components and the identification of the major predator species responsible for the mortality on each life stage of the pest (Stimac and O'Neil 1982). Once this information is obtained, the effects of changes in the species composition of the predator complex on the mortality imposed on a pest can be investigated (Stimac and O'Neil 1982).

To date, few studies have been conducted that employ field experimentation interspersed with systems modeling in an attempt to construct multipredator-prey models for predicting the impact of arthropod predators on pest population dynamics. The result has been a lack of methodology for obtaining the information required to take the first step in the construction of a multipredator-prey model. Therefore, this study was conducted to devise methods for and

to obtain quantitative estimates of rates of arthropod predation that would be consistent with those required for the construction of a multipredator-prey model. VBC was chosen as the experimental organism because of the damage it can inflict on Florida soybeans and because it typifies a noctuid pest in a row crop system.

In the following pages, an attempt is made to present the need for and to present a method for quantifying arthropod predation under field conditions. In the initial chapter, the life history of VBC is briefly reviewed. In the next 2 chapters, previous attempts to quantify arthropod predation in the field and to describe predation in terms of a general predator-prey model are critically reviewed. The proposed method for quantifying predation and the results of 3 years of its use are presented in the following 2 chapters. In the final chapters, the implications of the results on VBC population dyanmics and the general applicability of the method for quantifying arthropod predation are discussed.

Note

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LIFE HISTORY OF THE VELVETBEAN CATERPILLAR

VBC is a semitropical species found exclusively in the Western Hemisphere (Ford et al. 1975). Populations of VBC are common throughout the southern United States and occassionally may occur as far north as Maryland, Delaware, and Tennessee (Ford et al. 1975). This noctuid is also common throughout Central America, north and central South America, and the islands of the Caribbean (Ford et al. 1975).

VBC is an oligophagous species feeding primarily on the plants in the family Leguminosae (host range reviewed in Herzog and Todd 1980). With such feeding habits, VBC has gained notoriety as a pest of several leguminous crops, one of which is soybeans, Glycine max (L.) Merrill. In the tropics, VBC has long been regarded as a pest of soybeans (Turnipseed and Kogan 1976). With the recent expansion of soybean production in the semitropics, VBC is now regarded as the principal defoliating pest of soybeans in much of the tropics and semitropics of the Western Hemisphere (Turnipseed and Kogan 1976).

VBC adults migrate annually into the soybean producing areas of the southeastern United States. The moths are thought to migrate north from south Florida (Watson 1916, Buschman et al. 1981), and the Yucatan peninsula (Buschman et al. 1981). Studies

of VBC overwintering have suggested that in north Florida and areas north, VBC are unable to overwinter either by diapausing or by continuous breeding (Anonymous 1927, Watson 1932, Buschman et al. 1977b). The inability of VBC to diapause has never been demonstrated, but it has been noted that VBC cannot remain dormant during warm periods in mid winter (Anonymous 1927). Failure to maintain continuous breeding populations throughout the winter is hypothesized to be due to the frost sensitivity of host plants (Anonymous 1927, Buschman et al. 1977b). In north Florida, adult VBC begin to appear on available host plants in early May (Menke and Greene 1976, Buschman et al. 1977b) and invade soybeans by about the end of June (Anonymous 1927, Menke and Greene 1976). The larvae appear in soybeans in early to mid July (Neal 1974, Menke and Greene 1976) and attain their highest densities about the middle of August (Menke and Greene 1976), when soybean plants are in early bloom stage.

VBC eggs are laid singly on the underside of leaves, and on the stems and pods (Watson 1916, Greene et al. 1973). The eggs are placed between hairs on the surface of the plant (Greene et al. 1973). Under ambient temperature regimes characteristic of August (mean = 27.3°C) and September (mean = 25.8°C) in north Florida, egg hatch occurs about 3 days after oviposition (Watson 1916). Under constant temperature regimes of 32.2° and 26.7°C, egg hatch occurs at 3 days and 7 days after oviposition, respectively (Leppla et al. 1977).

VBC larvae can be found feeding upon the leaflets of soybean. The number of instars prior to pupation varies from 5-7 (Reid 1975) and is dependent upon temperature, host phenology (Reid 1975), and host plant (Reid 1975, Conti and Waddill 1982). The number of

days required to complete larval development varies from 11-53 days (Watson 1916, Reid 1975, Moscardi et al. 1981a, Oliveira 1981, Conti and Waddill 1982), depending upon temperature (Watson 1916, Reid 1975), host phenology (Reid 1975, Moscardi et al. 1981a, Oliveira 1981), and host plant (Reid 1975, Conti and Waddill 1982). The amount of foliage consumed by each instar has been reported by several authors (Watson 1916, Reid 1975, Boldt et al. 1975, Moscardi et al. 1981a, Oliveira 1981, Conti and Waddill 1982), and is also affected by temperature (Reid 1975), host phenology (Reid 1975, Moscardi et al. 1981a, Oliveira 1981), and host plant (Reid 1975, Conti and Waddill 1982).

Populations of VBC larvae demonstrate color polymorphism. Late in the season, darkly pigmented larvae ("dark" forms) become abundant within VBC populations. The polymorphism is hypothesized to be due to host quality (Watson 1916, Ellisor 1942).

Pupation occurs within the soil or in the litter on the soil surface (Watson 1916, Hinds 1930). The duration of the pupal stage varies with temperature, and in north Florida, it averages about 7 days in August (mean = 27.3°C) and about 10 days in September (mean = 25.8°C; Watson 1916).

VBC adults mate in the soybean canopy from about 2 hours after sunset to 2 am with peak mating activity occurring from 8 pm-10 pm (Greene et al. 1973). Oviposition also occurs at night with peak activity from 9 pm-11 pm (Greene et al. 1973). Females begin ovipositing 2-3 days after emergence (Leppla et al. 1977, Moscardi et al. 1981b, 1981c), and the number of eggs produced is dependent upon temperature (Moscardi et al. 1981b), and the phenological

stage of the host fed upon as an immature (Moscardi et al. 1981c, Oliveira 1981). Female adults have a mean longevity of 24.8 days and 11.2 days at 21.1° and 32.2°C, respectively (Moscardi et al. 1981b); adult males live approximately the same length of time (Leppla et al. 1977).

FIELD TECHNIQUES FOR QUANTIFYING ARTHROPOD PREDATION

Introduction

The importance of predator complexes, or interacting groups of arthropod predator species that function as a unit in inflicting mortality, in pest population regulation has long been recognized. Prior to the use of insecticides, researchers recognized the contribution of arthropod predators by listing the common predator species within a complex in descriptions of the life history of a pest (e.g., Dew 1913, Hinds and Dew 1915, Watson 1916, Luginbill 1928, Douglas 1930, Hinds 1930, Wilson 1932). After the use of insecticides became common practice, it was found that population densities of target pests were sometimes larger in insecticide treated fields than in untreated fields. Ewing and Ivy (1943) found this to be true of densities of bollworm, Heliothis zea (Boddie), eggs and larvae in plots of cotton dusted with arsenicals. To explain the larger densities in treated fields, they proposed 3 hypotheses. The first hypothesis was that in dusted fields, there was an excess of honeydew produced by large densities of aphids that served as an attractant to bollworm moths. This increased the density of ovipositing bollworm females within a treated field. The second hypothesis was that predators that fed on aphids and bollworm eggs

and larvae were killed by the arsenical insecticide. Without predation pressure, pest populations could increase rapidly. The third hypothesis was that the predators ate more aphids than bollworms, especially when aphid populations increased after insecticide application. As the aphids became more abundant, bollworm populations could also increase because of reduced predation pressure caused by a preference of arthropod predators for aphids. Ewing and Ivy (1943) concluded that the third hypothesis adequately explained the differences in bollworm population densities in treated and untreated fields. However, they failed to propose hypotheses concerning increases in aphid population densities after insecticide treatment, other than to say it was not caused solely by the removal of predators. In another study of the effect of insecticides on arthropod predators in cotton, Newsom and Smith (1949) found that the second hypothesis proposed by Ewing and Ivy (1943) more adequately explained differences in pest populations in treated and untreated fields. Newsom and Smith found that the timing of insecticide application, in addition to the insecticide used and a complex of other factors, greatly influenced the effect of insecticides on predator populations. In more recent years, similar results were obtained in numerous studies of the impact of insecticides on predator populations in alfalfa, cotton, and soybeans (e.g., Smith and Hagen 1959, Stern and van den Bosch 1959, Harrison 1960, Pfrimmer 1964, Laster and Brazzel 1968, Falcon et al. 1968, Dinikins et al. 1971, Eveleens et al. 1973, Ehler et al. 1973, Keever et al. 1977, Marston et al. 1979, Brown and Goyer 1982).

Having recognized the importance of arthropod predators in pest population dynamics, numerous life history studies were conducted on some of what were deemed to be the most "important" predator species within a complex. A sample of some of these life history studies on some of the more common predator species within row crops is listed in Table 1. These studies include studies on life cycle, feeding habits, oviposition, behavior, and diapause.

The information obtained in life history studies provides a foundation on which to build a quantitative description of arthropod predation. This description, however, requires considerably more information than that contained in life history studies. Several methods have been proposed to provide the additional information required to quantify and describe the mortality inflicted on pests of row crops by arthropod predators. The methods include surveys of predator populations, mark-release-recapture, direct observation, and serological techniques, and manipulation of predator and prey populations (Whitcomb 1981). The literature associated with these techniques is immense. Therefore, in the following discussion the literature reviewed will be limited to studies of predation on insects inhabiting row crops (for a more general discussion see Kiritani and Dempster 1973).

Surveys of Predator Populations

Surveys of predator populations are useful to identify predator species that have the potential to feed on a given prey species and to determine the relative abundances of predator species over time

Table 1. A sample of studies of life histories and components of life history of the more common row crop predators.

Family	Species	Reference
ARANEAE		
Oxyopidae	Oxyopes salticus Hentz	Whitcomb and Eason 1967
	Peucetia viridans (Hentz)	Whitcomb et al. 1966
		Turner 1979
Clubionidae	Chiracanthium inclusum (Hentz)	Peck and Whitcomb 1970
Lycosidae	Lycosa punctulata Hentz	Eason and Whitcomb 1965
	Pardosa ramulosa (McCook)	Leigh and Hunter 1969
		Yeargan 1975
Salticidae	Phidippus audax (Hentz)	Bailey 1968
	Metaphidippus galathea (Walckenaer)	Horner and Starks 1972
Thomisidae	Misumenops celer (Hentz)	Muniappan and Chada 1970
	Misumenops deserti Schick	Leigh and Hunter 1969
	Xysticus californicus Keyserling	Leigh and Hunter 1969
Linyphiidae	Erigone dentosa Cambridge	Leigh and Hunter 1969
DERMAPTERA		
Labiduridae	Labidura riparia (Pallas)	Schlinger et al. 1959
		Shepard et al. 1973

Table 1. continued.

Family	Species	Reference
DERMAPTERA		
Labiduridae	Euboriella cincticollis (Gerstaecker)	Knabke and Grigarick 1971
	Euboriella annulipes (Lucas)	Klostermeyer 1942
HEMIPTERA		
Anthocoridae	Orius tristicolor (White)	Askari and Stern 1972
		Salas-Aguilar and Ehler 1977
	Orius insidiosus (Say)	Garman and Jewett 1914
		Barber 1936
		Isenhour and Yeargan 1982
		Kingsley and Harrington 1982
Lygaeidae	Geocoris punctipes (Say)	Champlain and Sholdt 1967a
		Champlain and Sholdt 1967b
		Crocker 1977
		Crocker et al. 1975
		Dunbar and Bacon 1972
	Geocoris pallens Stål	Tamaki and Weeks 1972a
		Ridgway and Jones 1968

Table 1. continued.

Family	Species	Reference
HEMIPTERA		
Lygaeidae	Geocoris bullatus (Say)	Tamaki and Weeks 1972a
		Sweet 1960
	Geocoris uliginosus (Say)	Sweet 1960
	Geocoris spp.	Readio and Sweet 1982
Nabidae	Nabis ferus (L.)	Garman and Jewett 1914
		Knowlton 1949
	Nabis alternatus Parshley	Knowlton 1943
		Taylor 1949
		Perkins and Watson 1972
		Stoner 1972
		Stoner et al. 1975
	Nabis americoferus Carayon	Ridgway and Jones 1968
		Stoner 1972
		Stoner et al. 1975
		Isenhour and Yeargan 1982
	Nabis roseipennis Reuter	Isenhour and Yeargan 1982

Table 1. continued.

Family	Species	Reference
HEMIPTERA		
Nabidae	Tropiconabis capsiformis (Germar)	Hormchan et al. 1976 b
		Stoner 1972
		Stoner et al. 1975
Miridae	Spanogonicus albofasciatus (Reuter)	Butler and Stoner 1965
		Butler 1965
Pentatomidae	Podisus acutissimus Stal	Stoner et al. 1974
	Podisus maculiventris (Say)	Warren and Wallis 1971
		Richman and Whitcomb 1978
	Stiretrus anchorago (F.)	Waddill and Shepard 1974
		Richman and Whitcomb 1978
	Alcaeorrhynchus grandis (Dallas)	Richman and Whitcomb 1978
	Euthyrhynchus floridanus (L.)	Richman and Whitcomb 1978
COLEOPTERA		
Carabidae	Lebia spp.	Hemenway and Whitcomb 1967
Malachiidae	Collops vittatus (Say)	Nielson and Henderson 1959
Coccinellidae	Predaceous coccinellids	Hagen 1967
	Coleomegilla maculata (DeGeer)	Garman and Jewett 1914

Table 1. continued.

Family	Species	Reference
COLEOPTERA		
Coccinellidae	Hippodamia convergens (G.-M.)	Nielson and Currie 1960
		Miller and Thompson 1927
	Leis spp.	Thompson 1926
	Cycloneda sanguinea immaculata (F.)	Miller and Thompson 1927
	Olla abdominalis sobrina Casey	Miller and Thompson 1927
	Exochomus marginipennis childreni Muls.	Miller and Thompson 1927
HYMENOPTERA		
Vespidae	Polistes metricus Say	Pellet 1916
	Polistes spp.	Rabb and Lawson 1957
		Rabb 1960

and/or space. Surveys usually take 1 of 2 forms: surveys of single or small groups of predator species, or surveys that attempt to sample all predator species found in a given area or habitat. Examples of surveys done on a single species or select group of predator species can be found in Table 2. In these studies, data were obtained from a variety of techniques that included sweep net, ground cloth, pitfall traps, D-Vac® samplers, and direct observation. In some of these studies, the relative abundance of each predator species was determined. In addition, the distribution of the predator species through space was examined by Whitcomb et al. (1963b), Neal and Whitcomb (1972), Shepard et al. (1974b), Waddill et al. (1974), Waddill and Shepard (1975), LeSar and Unzicker (1978), Wilson and Gutierrez (1980), and Bechinski and Pedigo (1981b).

Examples of surveys of total predator species found in a given area or habitat are presented in Table 3. The purpose of the study, to determine relative abundance and/or to identify the predator species present, is also indicated. The techniques used to sample the predator populations in these surveys are similar to those listed above.

Most of the surveys presented were conducted within the confines of the host crop field and/or during the growing season of the host crop, and therefore give no indication as to the sources of predators found within the field. Such information is important in understanding predator movement and the initial colonization of fields of row crops by arthropod predators. A few surveys have been conducted to investigate the possible sources of arthropod predators. These include surveys of potential overwintering sites of selected species

Table 2. A summary of surveys of single or small group of species of predaceous arthropods.

Predator	Host crop	Location	Reference
Misumenops celer (Hentz)	alfalfa	Oklahoma	Muniappan and Chada 1970
Pardosa ramulosa (McCook)	alfalfa	California	Yeargan and Cothran 1974
Araneae	alfalfa	New York	Wheeler 1973
Araneae	alfalfa	California	Yeargan and Dondale 1975
Araneae	pasture and cotton	Arkansas	Whitcomb et al. 1963 a
Araneae	cotton	Arkansas	Whitcomb et al. 1963 b
Araneae	cotton	California	Leigh and Hunter 1969
Araneae	soybeans	Illinois	LeSar and Unzicker 1978
Araneae	cotton	Texas	Kagan 1943
Odonata	soybeans	Florida	Neal and Whitcomb 1972
Labidura riparia (Pallas)	soybeans, corn, cotton, pasture, and woodlands	South Carolina	Walker and Newman 1976
Labidura riparia (Pallas)	soybeans	South Carolina	Price and Shepard 1977
Labidura riparia (Pallas)	cabbage	Florida	Strandburg 1981 a
Hemiptera	alfalfa	California	Benedict and Cothran 1975
Spanogonicus albofasciatus (Reuter)	soybeans	Florida	Neal et al. 1972

Table 2. continued.

Predator	Host crop	Location	Reference
Miridae	alfalfa	New York	Wheeler 1974
Orius insidiosus (Say)	corn	Virginia	Barber 1936
Orius insidiosus (Say)	corn	Ohio and Iowa	Dicke and Jarvis 1962
Orius insidiosus (Say)	soybeans	Missouri	Isenhour and Yeargan 1981
Geocoris pallens Stäl and Geocoris bullatus (Say)	sugar beets, pea, broccoli, alfalfa, and potato	Washington	Tamaki and Weeks 1972a
Nabis alternatus Parshley, Nabis americoferus Carayon, and Tropiconabis capsiformis (Germar)	alfalfa	Arizona	Stoner et al. 1975
Nabis alternatus Parshley, Nabis roseipennis Reuter, Tropiconabis capsiformis (Germar), Hoplistoscelis deceptivus (Harris), and Hoplistoscelis sordidus (Reuter)	cotton, alfalfa, and grasslands	Mississippi	Hormchan et al. 1976a
Carabidae	corn and prairies	Iowa	Esua and Peters 1975
Carabidae	agricultural fields	Ontario	Rivard 1964, 1965
Lebia spp.	cotton	Arkansas	Whitcomb and Bell 1960

Table 2. continued.

Predator	Host crop	Location	Reference
Calosoma sayi DeJean	soybeans	South Carolina	Price and Shepard 1978
Formicidae	soybeans	Florida	Whitcomb et al. 1972
Chrysopa spp., Geocoris spp., and Nabis spp.	cotton	Mississippi	Dinikins et al. 1970
Nabis spp., Orius insidiosus (Say), and Geocoris spp.	soybeans	Kentucky	Raney and Yeargan 1977
Chrysopa carnea Stephens, Geocoris pallens Stal, Geocoris punctipes (Say), Orius tristicolor (White), and Nabis americoferus Carayon	cotton	California	Wilson and Gutierrez 1980
Nabis spp., Geocoris spp., Orius spp., and Araneae	soybeans	Virginia	McPherson et al. 1982

Table 3. A sample of surveys of arthropod predators in which a large number of species were sampled.

Habitat	Location	Purpose of Study[a]	Reference
Verbena spp, mixed grasses, sunflowers, vervains, *Nicotiana* spp., grain sorghum, and citrus	Texas	A,I	Fuchs and Harding 1976
Multiple crops[b]	Florida	A,I	Martin 1976
Alfalfa	New York	A,I	Wheeler 1977
Cotton	Arkansas	A,I	Whitcomb and Bell 1964
Cotton	Texas	A	Shepard et al. 1972
Soybeans and cotton	Mississippi	A	Pitre et al. 1978
Soybeans	Minnesota	I	Kretzschmar 1948
Soybeans	Missouri	A,I	Bickenstaff and Huggans 1962
Soybeans	Missouri	A	Barry 1973
Soybeans	Missouri	A	Ignoffo et al. 1976
Soybeans	Missouri	A,I	Marston et al. 1979
Soybeans	Florida	A,I	Hasse 1971
Soybeans	Florida	A,I	Neal 1974
Soybeans	South Carolina	A,I	Shepard et al. 1974a

Table 3. continued.

Habitat	Location	Purpose of Study[a]	Reference
Soybeans	North Carolina	A,I	Deitz et al. 1976
Soybeans	Illinois	A,I	Mayse and Price 1978
Soybeans	Delaware	A	Culin and Rust 1980
Soybeans	Iowa	A,I	Bechinski and Pedigo 1981a

[a]A = study of abundance of species; I = identification of species

[b]Includes collards, cabbage, soybeans, tobacco, okra, white clover, corn sorghum, millet, field peas, peanuts, bell peppers, rye wheat, tomatoes, turnips, pumpkins, bush beans, squash, Bahia grass and roadside weeds

of coccinellids (reviewed in Hagen 1967) and pentatomids (Jones and Sullivan 1981), and groups of predator species (Martin 1976, Fuchs and Harding 1976).

Surveys do not give information that can be directly transformed into a given amount of predation. Nevertheless, surveys of predator populations are important for building quantitative descriptions of arthropod predation because of their utility in identifying the species comprising the complex, determining the relative abundance of each predator species, quantitatively describing insect movement, and determining seasonal abundance and spatial variation. All this information is required in a complete quantitative description of predation.

Mark-Release-Recapture Techniques

Mark-release-recapture techniques allow estimation of the total mortality of a prey species occurring over a given period of time. A variety of marking schemes is available for marking insects (reviewed in Walker and Wineriter 1981), but the most commonly used in mortality studies are fluorescent pigments and radioisotopes. Luna (1979) used yellow Day-Glo® dust to mark second and third instar VBC larvae in a mortality study. He found that the fluorescent dye was inadequate as a marker because the larvae would molt during the experiment, thereby shedding the pigment. He recommended the use of an internal marker such as a radioisotope for mortality studies. Cook and Kettlewell (1960) were some of the first researchers to use radioisotopes as markers in mortality studies. They found they

could easily mark lepidopterous larvae with radioactive phosphorous (^{32}P), and by recapturing adults, were able to estimate the total mortality occurring in late larval and pupal stages. Buschman et al. (1977a) also used ^{32}P to mark VBC eggs in order to determine the total egg mortality occurring in 24 hours.

In some mortality studies, the location of prey was marked rather than the prey themselves. Fletcher and Thomas (1943) marked the location of naturally occurring bollworm, H. zea, eggs and first instar larvae in cotton, so that daily observations of eggs and larvae could be made. From these observations, they were able to estimate stage specific mortality. In a similar study of predation mortality on bollworm eggs on corn, Harrison (1960) was able to estimate the stage specific predation mortality and assign this mortality to 1 of 3 species of predators. Harrison was able to assign the predation mortality based upon examination of the remains of eggs because from laboratory studies with the 3 predator species, he found that the damage inflicted by each species was characteristic of that species. Bell and Whitcomb (1962, 1964) modified Harrison's technique to examine the mortality inflicted on bollworm eggs in cotton. To do this, they released known densities of unmarked eggs at specific locations within the cotton fields. The eggs were examined at variable time intervals after release. The predators responsible for the mortality were grouped according to type of mouthparts because Bell and Whitcomb could not distinguish the feeding damage of individual predator species with similar feeding habits. The feeding activity of predators with sucking mouthparts gave the remains of the eggs a tepee shape, whereas

the feeding activity of those predators with chewing mouthparts resulted in collapsed or missing eggs. This technique for assigning the mortality to groups of predators has also been used in mortality studies of eggs of H. virescens (F.) (Elsey 1972, Agnew et al. 1982), eggs of pink bollworm, Pectinophora gossypiella (Saunders) (Henneberry and Clayton 1982), eggs of several pentatomids (Yeargan 1979), larvae of the cotton boll weevil, Anthonomus grandis (Boheman) (Sterling 1978), pupae of the pickle worm, Diaphania nitidalis (Stöll) (Elsey 1980), and pupae of the cabbage looper, Trichoplusia ni (HÜbner) (Strandberg 1981b).

To determine the predator species responsible for the mortality inflicted on a prey species, radioisotopes, in particular ^{32}P, have been used as a marker in mark-release-recapture studies. By releasing radioactive prey within a field, the predator species inflicting mortality can be identified by tracing the flow of ^{32}P through the food chain. McCarty et al. (1980) used the releases of ^{32}P marked eggs to determine the predators feeding upon eggs of H. zea, H. virescens, Pseudoplusia includens (Walker), and A. gemmatalis in soybeans. They used autoradiography to determine if field collected predators contained any radioactive materials. In a similar study, Buschman et al. (1977a) used VBC eggs marked with ^{32}P to determine the predator species feeding upon VBC eggs in soybeans. They counted the radioactivity contained in field collected predators. From this, they could estimate the maximum number of eggs consumed by dividing the mean counts per minute (cpm) found in the predator by the mean cpm of VBC eggs.

McDaniel and Sterling (1979) did a similar study using ^{32}P marked H. virescens eggs in cotton. They used the following formula to calculate the number of eggs consumed per predator:

No. consumed = $(CPI_t - B)/(E)(MC)(DPM_{egg})(D_t)$

where CPI = counts per insect at time t, B = background of counter (20 CPI), MC = minutes sample counted (10), E = counter efficiency (mean = 0.28), DPM_{egg} = radioactive disintegrations per minute of the egg, D_t = decay time for time t. Use of this formula for calculating the number of prey consumed by a predator species over time is based on 3 assumptions. The first assumption is that each prey item released in the field contains the same amount of ^{32}P. McDaniel et al. (1978) devised an injection technique to insure uniformity of egg radioactivity. The second assumption is that predators become radioactive only after feeding on marked prey (i.e., no secondary contamination). Evaluation of this assumption was not attempted. The final assumption is that the amount of radioactivity consumed by a predator in a meal is detectable for a very short period of time. In other words, the biological half-life of the radioisotope in the predator is very small. For example, if the predator eats 1 marked prey at release time 1 and does not consume any more marked prey, the amount of radioactivity in that predator at release time 2 will be negligible. To date, no studies on the biological half-life of radioisotopes in predator species having consumed differing amounts of prey have been published.

In a continuation of this study, McDaniel and Sterling (1982) also determined the amount of mortality occurring on marked H.

virescens eggs. By excluding various groups of predators from some release sites, they were able to estimate the daily total mortality and the mortality attributable to various groups of predators. The species included in each group were also identified.

In quantifying arthropod predation, mark-release-recapture techniques are most valuable for estimating rates of mortality over a given period of time. Use of the techniques to obtain information other than mortality estimates is based upon either subjective classification of the predtors inflicting mortality, or on assumptions whose validity is questionable. Therefore, mark-release-recapture techniques should be used to obtain estimates of mortality rates rather than to trace the flow of energy through the food chain.

Direct Observation Technique

Direct observation provides information on the predator species regularly feeding on a prey species, and the proportion of prey consumed by a given predator species. This technique was originally devised to determine the number of eggs consumed over time, and which predators were consuming eggs. In its early form as used by Bell and Whitcomb (1962, 1964), it was simply a mark-release-recapture technique in which H. zea eggs were placed on cotton foliage and were collected 24 hours later. The eggs were then categorized as having been consumed by predators with chewing mouthparts, predators with sucking mouthparts, or as missing eggs. At the same time as the eggs were released in the field, collections

of predators were made. The predators were categorized as having sucking or chewing mouthparts. Bell and Whitcomb (1964) were unable to find any correlation between abundance of a single predator species and the number of eggs consumed. They stated that this failure was due to the inability to distinguish the feeding of different species. To overcome this difficulty, the technique was modified so that an observer sat in the field and watched the prey after release onto the foliage. The results of using the modified technique to determine the arthropod predators of H. zea and H. virescens eggs in cotton were reported in Lincoln et al. (1967) and Whitcomb (1967a) and the predators of second instar H. zea larvae in Whitcomb (1967b). The technique was further modified for observing H. zea larvae in cotton, and this modified technique was also used for observing VBC larvae in soybeans. In this modification, the observer lay on his back between the rows and watched the released larvae (W. H. Whitcomb, personal communication)[1]. This modification proved to be very labor-intensive and extremely exhausting to the observer. Therefore, the technique evolved to the current version in which an observer moves from one release site to another and records predation observed (W. H. Whitcomb, personal communication)[2].

The use of the direct observation technique for determining the predator species regularly feeding upon a prey species and the proportion of prey consumed by a predator species assumes that the presence of the observer does not affect the behavior of arthropod predators. It further assumes that the predation observed on released prey at an observation station is representative of that

occurring throughout the field. The validity of both assumptions remains to be determined.

Direct observation is a useful technique for identifying the key predator species within a complex when attempting to understand and quantify predation. This technique requires little equipment and can be modified to accomodate the characteristics of most communities, given adequate labor resources. The information obtained from direct observation studies must be used cautiously because of the difficulty in evaluating the validity of its assumptions.

Serological Techniques

Serological techniques use the antigen-antibody reaction to detect the presence of prey in the gut of the predator. In doing so, these techniques provide information on the predator species responsible for the mortality inflicted on prey populations. The more commonly used techniques for examining predator-prey relations in field crops are the precipitin test and the enzyme-linked immunosorbent assay (ELISA). The procedures for each technique are reviewed in Boreham (1979) and Fitcher and Stephen (1979).

Precipitin tests were first used to identify the predators of immature mosquitoes and were later adapted for use with insect pests of row crops (reviewed in Boreham and Ohiagu 1978, and Frank 1979). Precipitin tests have been used to determine the arthropod predators regularly feeding on the following insect pests: the introduced wireworm, Agriotes sputator (L.) (Fox and

McLellan 1956), the cabbage maggot, Hylemya brassicae (Bouché) (Coaker and Williams 1963), the cabbage butterfly, Pieris rapae (L.) (Dempster 1967, Ashby 1974), the rice-ear bug, Leptocorisa oratorinus F. (Rothschild 1970), the red-backed cutworm, Euxoa ochrogaster Guenée (Frank 1971), aphids in cereal crops (Vickerman and Sunderland 1975), and a complex of noctuids in soybean, A. gemmatalis, H. zea, and P. includens (Gardner et al. 1981). In some studies, cross reactivity among antigen preparations of stages (Frank 1971, Coaker and Williams 1963) and of species (Fox and McLellan 1956, Dempster 1967, Vickerman and Sunderland 1975, Gardner et al. 1981) was noted. This cross reactivity limited the ability of the test to discriminate predator species that were preying upon a particular stage or species.

ELISA has greater sensitivity than the precipitin test (Boreham 1979). This sensitivity is imparted by linking an enzyme to a host-specific antibody. The enzyme provides a means by which the antibody-antigen reaction can be amplified.

ELISA has been utilized in the study of predators of only 1 field crop pest, Nezara viridula (L.) (Ragsdale et al. 1981). In their study, Ragsdale et al. (1981) derive an index of predator efficiency based on the percent positive responses by a predator species obtained in an ELISA and the predator density. This index purports to measure the percent predation on N. viridula contributed by each species within the complex. Calculation of the index required assumptions on the number of prey consumed at each meal and the length of time a meal was detectable.

In understanding and quantifying predation, serological techniques are valuable in identifying predator species and determining the proportion of prey consumed by a given predator species. The information obtained from the use of these techniques is similar to that obtained by direct observation. However, the serological techniques have the advantage of identifying predator species whose behaviors would otherwise exclude them from being observed. Unfortunately, serological techniques have several disadvantages. These include the requirement of specific antisera, the inability to discriminate between scavenging and predation, and the equipment and facilities required to use serological techniques.

Manipulation of Prey and Predator Populations

The manipulation of prey and predator populations allows the estimation of the number of prey taken by each predator species over time with a known density of prey and predators. Several methods have been used to manipulate prey and predator populations. These include inhibiting flight and dispersal of predators, and field cage studies of predator-prey relationships.

To estimate predation inflicted on a population of green peach aphid, Myzus persicae (Sulzer), by a complex of predators, Tamaki and Weeks (1973) inhibited the flight and dispersal of individuals of Geocoris pallens Stäl, G. bullatus (Say), Nabis americoferus Carayon, N. alternatus Parshley, Coccinella transversoguttata Falderman, and Hippodamia convergens Guérin-Meneville, by gluing the wings of each individual predator. They then released the

predators into sugar beets infested with green peach aphid. After a period of time, the density of green peach aphid populations in each plot of sugar beets was estimated. Tamaki and Weeks found that the plots treated with flightless predators had statistically lower populations of aphids than the control plots or those plots from which predators were excluded. They attributed the lower numbers to a combination of the removal of predators from control plots, addition of flightless predators, and the effect of the naturally established predator complex already present within the field.

In numerous other studies, the amount of mortality inflicted by arthropod predators was estimated by manipulating densities of prey and predator populations within field cages (studies summarized in Table 4). In most of these studies, rates of prey consumption were estimated for a single species of predator. In a few studies, such rates were determined for a complex of predators composed of 2 or more species (van den Bosch et al. 1969, Barry et al. 1974, Collins 1980, Frazer et al. 1981). In all of the studies, except Collins (1980) and Frazer et al. (1981), the densities of prey and predator populations were unrealistic with respect to field densities. The high rates of prey consumption found in these studies, therefore, may not be representative of such rates within the field in the absence of field cages.

Two of the studies listed in Table 4 are particularly notable. The first is that of Collins (1980) who estimated the consumption rates of a complex of predators on soybean looper, P. includens,

Table 4. Field cage studies involving the manipulation of prey and predator populations.

Prey	Predator	Host Crop	Purpose of Study[a]	Reference
Heliothis zea (Boddie)	Geocoris pallens Stål Nabis americoferus Carayon Chrysopa carnea Stephens	cotton	C,R	van den Bosch et al. 1969
Heliothis zea (Boddie) and H. virescens (F.)	Hippodamia convergens G.-M. Chrysopa carnea Stephens Chrysopa rufilabris Burmeister Scymnus hortensis Wingo Scymnus loweii Mulsant Nabis alternatus Parshley Geocoris punctipes (Say) Geocoris uliginosus (Say) Orius insidiosus (Say) Collops vittatus (Say) Collops balteatus LeConte Zelus renardii Kolenati Oxyopes salticus Hentz	cotton	C	Lingren et al. 1968
Heliothis zea (Boddie) and H. virescens (F.)	Chrysopa carnea Stephens Geocoris punctipes (Say) Coleomegilla maculata (DeGeer) Podisus maculiventris (Say)	cotton	C	Lopez et al. 1976

Table 4. continued.

Prey	Predator	Host Crop	Purpose of Study[a]	Reference
Heliothis zea (Boddie) and Trichoplusia ni (Hubner)	Nabis alternatus Parshley Geocoris punctipes (Say) Chrysopa carnea Stephens	soybean	C,R	Barry et al. 1974
Pectinophora gossypiella (Saunders)	Chrysopa carnea Stephens Geocoris pallens Stal Geocoris punctipes (Say) Nabis americoferus Carayon Notoxus calcaratus Horn Orius tristicolor (White) Spanogonicus albofasciatus (Reuter)	cotton	C	Irwin et al. 1974
Anticarsia gemmatalis Hbn. and Pseudoplusia includens (Wlk.)	Peucetia viridans (Hentz) Podisus maculiventris (Say) Tropiconabis capsiformis (Germar) Labidura riparia (Pallas) Hentzia palmarum (Hentz) Oxyopes salticus Hentz Calleida decora (F.)	soybean	R	Collins 1980

Table 4. continued.

Prey	Predator	Host Crop	Purpose of Study[a]	Reference
Pseudoplusia includens (Wlk.)	Nabis roseipennis Reuter Tropiconabis capsiformis (Germar) Hoplistoscelis deceptivus (Harris) Geocoris uliginosus (Say) Geocoris punctipes (Say) Geocoris bullatus (Say) Hentzia palmarum (Hentz) Oxyopes salticus Hentz Chrysopa rufilabris Burmeister Chiracanthium inclusum (Hentz) Metaphidippus galathea (Walckenaer) Calleida decora (F.) Labidura riparia (Pallas) Stiretrus anchorago (F.) Podisus maculiventris (Say) Arilus cristatus (L.)	soybean	C	Richman et al. 1980
Acyrthosiphon pisum (Harris)	Indigenous arthropod predator complex	alfalfa	R	Frazer et al. 1981

[a] C = comparison of consumption rates of individual predator species; R = response of predator complex to various prey densities

and VBC, A. gemmatalis, larvae using prey and predator densities similar to those found in the field. He found that a predator complex could act as a functional unit and demonstrate a functional response. He also noted that some predator species would feed upon other predators when prey densities were low.

The second of the 2 studies is that of Frazer et al. (1981) who examined the impact of an indigenous arthropod predator complex on the dynamics of populations of pea aphid, Acyrthosiphon pisum (Harris), in alfalfa. By excluding indigenous arthropod predators with field cages, they found increases in the densities of pea aphid populations within the cages that could not be attributed to increases in aphid fecundity alone. They believed that the absence of predators also contributed to the increases in aphid populations. By selectively placing and removing field cages, they also demonstrated the importance of predator movement in limiting prey population densities.

Manipulation of prey and predator populations within field cages has utility in examining the effects of prey density, predator density, and the species composition of the predator complex on rates of arthropod predation. However, the effects of these factors can be investigated more realistically once an indigenous arthropod predator complex and the mortality it imposes can be characterized quantitatively. In the meantime, field cage studies serve to stress the importance of arthropod predators in prey population dynamics.

Of the methods presented, none alone provides the information required to derive a quantitative description of the impact of

arthropod predators on the dynamics of pests of row crops. In addition, the information obtained from the use of the method was not structured in such a way as to allow assessment of the impact of arthropod predation. To obtain the required information and to structure this information requires a coupling of experimentation and modeling. From such a coupling, an initial predator-prey model can be constructed from a quantitative description of predation which includes estimates of predation mortality, identification of the species responsible for that mortality, and estimates of the densities of various predator species within the field. This information can be obtained from the use of a combination of the methods discussed in this chapter. With further experimentation, the initial model can be validated and expanded to include more biological mechanism. This validation and expansion of the model cna result in the construction of a powerful tool for predicting the impact of arthropod predators on prey population dynamics and/or investigating mechanisms of pest population regulation.

Notes

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MODELS OF PREDATION

Introduction

Understanding the role of arthropod predators in prey population dynamics requires quantitative descriptions of arthropod predation. In the previous chapter, many studies were presented in which attempts were made to quantify the role of arthropod predators. The results from these studies, however, did not provide the information or a structuring of the information that would allow examination and comprehension of predator-prey dynamics. Structuring the information once it is obtained is facilitated by the construction of a predation model or simplistic representation of the process of predation. Models of predation provide a means by which the mechanisms governing arthropod predation can be investigated and understood.

Numerous arthropod predator-prey models have been constructed. Essentially, these models fall into 2 categories. The first category includes the general predator-prey models that attempt to describe the behavior of predator-prey dynamics common to all arthropod predator-prey interactions. The second category of predation models includes empirical models that attempt to describe the role of 1 or more arthropod predator species on a single prey species or small group of prey species within a particular system. These models

were developed in response to the inadequacy of the general predator-prey models for describing predation under field conditions.

The literature associated with arthropod predator-prey models is extensive. Therefore, in the following discussion, the classic predator-prey models from which most other predator-prey models were derived will be reviewed. Several of the general predator-prey models were formulated as parasite-host models, but because of the similarity between parasite-host and predator-prey interactions, only minor modifications of the models are required to adapt them for describing predator-prey interactions. The general models included in the review are the Lotka-Volterra, Nicholson-Bailey, and Hassell-Varley models. In addition, the few empirical models of arthropod predation that attempt to describe arthropod predation on pests of row crops and the Holling functional response model will be reviewed. The mathematics associated with the models will be kept to a minimum, and references to discussions of the mathematics will be provided.

Lotka-Volterra Model

The Lotka-Volterra model, the first model of predator-prey dynamics, was derived independently by Lotka (1925) and Volterra (1931). The model, using Lotka's notation, is

$$\frac{dN_1}{dt} = r_1N_1 - kN_1N_2$$

$$\frac{dN_2}{dt} = KN_1N_2 - d_2N_2$$

where N_1 is the number of prey, r_1 is the rate of increase of prey ($r_1 = b_1 - d_1$, where b_1 is the per capita birth rate, and d_1 is the per capita death rate from mortality agents other than predators), kN_1N_2 is the death rate of prey due to predators, N_2 is the number of predators, KN_1N_2 is the predator per capita birth rate ($KN_1N_2 = k'kN_1N_2$, where k' is a function of the number of prey consumed required to produce 1 predator), and d_2 is the predator per capita death rate.

This model is based on 5 assumptions. The first assumption is that the rate of increase of the prey is exponential in the absence of predation pressure (i.e., r_1 = constant). This implies that the resources, such as food, shelter, and mates, available to the prey are unlimited. The second assumption is that a constant proportion of prey is killed and consumed by predators (i.e., k = constant) which implies that predators never become satiated. The third assumption is that the number of prey required by a predator to produce 1 progeny (k') is constant. The fourth is that the predator per capita death rate (d_2) is also constant. The final assumption is that predators have unlimited searching capacity in a searching universe which has a constant area through time. The formulation of this model as differential equations further implies that there are no time lags in the production of new predators or prey. All of these assumptions are unrealistic biologically, but are necessary to preserve mathematical simplicity.

The Lotka-Volterra model predicts cyclic fluctuations of predator and prey populations of uniform amplitude (i.e., limit cycles). Such cycles have been demonstrated by vertebrate predator

and prey populations (e.g., the snowshoe hare-lynx populations, Elton and Nicholson 1942). Unofrtunately, these population cycles have not been demonstrated to be caused solely by predation (Wangersky 1978).

The Lotka-Volterra model of predator-prey interaction is inadequate to describe arthropod predator-prey interactions under field conditions. By having its origins in the laws of mass action, the Lotka-Volterra model largely ignores many biological and behavioral attributes characteristic of natural predator-prey populations. To formulate a model that realistically describes predator-prey interactions, these attributes must be incorporated (Stimac 1981).

Nicholson-Bailey Model

The Nicholson-Bailey model incorporates more biological mechanisms than the Lotka-Volterra model. In their model, Nicholson and Bailey (1935) included a parameter called "the area of discovery" which accounts for the searching efficiency of a parasite or predator. The area of discovery is defined as the average area that a parasite or predator searches in its lifetime. The average value was assumed by Nicholson to represent the area of discovery for a given species.

In its original formulation, the Nicholson-Bailey model attempted to describe the dynamics of parasite-host interactions. Nicholson (1933) recognized that this model could be utilized to describe the dynamics of predator-prey interactions given certain modifications. These modifications included the addition of model structure to

take into account the age structure of a predator population and to describe predator reproduction more realistically. The model, formulated as a pair of difference equations is

$$N_{t+1} = \lambda N_t e^{(-aP_t)}$$

$$P_{t+1} = N_t(1 - e^{(-aP_t)})$$

where N_{t+1} is the number of hosts at time t+1, λ is the intrinsic rate of increase of the host, N_t is the number of hosts at time t, a is the area of discovery, P_t is the number of parasites at time t, P_{t+1} is the number of parasites at time t+1, and $e^{(-aP_t)}$ is the fraction of hosts surviving parasitism.

This model is based on the following 5 assumptions:

1. the number of encounters by hosts by parasites is in direct proportion to host density,
2. encounters are distributed at random among available hosts (i.e., search is random),
3. the rate of increase of the host is constant (i.e., λ is constant),
4. the area of discovery is constant and species specific,
5. one parasitized host at time t results in 1 parasite at time t+1.

The first 2 assumptions imply that parasites and predators do not change their searching behavior once a host or prey has been contacted, or that they demonstrate any aggregative response. Clearly, these assumptions greatly oversimplify parasite and predator behavior because parasites and predators have been shown to change their searching behavior after contact with a host or prey (e.g., Salt

1934a, 1934b, 1935, Turnbull 1964, Ives 1981b) and parasites and predators will demonstrate aggregative responses (Solomon 1949, Hassell 1966, 1978). The third assumption implies that the host population exists in an unlimited environment, and in the absence of parasitism or predation pressure, host or prey numbers will increase exponentially. The fourth assumption presupposes an unlimited egg supply in the parasite or unlimited gut capacity in the predator. The final assumption implies that there are no time lags between the parasitism of a host or consumption of a given number of prey and the production of parasites or predators.

The Nicholson-Bailey model predicts population oscillations that increase in amplitude. This results in the extinction of 1 population. In laboratory studies, population cycles of Musca domestica L. and its parasite, Nasonia vitripennis (Wlk.) (DeBach and Smith 1941), Eotetranychus sexmaculata (Riley) and its predator, Typhlodromus occidentalis Nesbitt (Huffaker 1958), and Trialeurodes vaporariorum (Westwood) and its parasite, Encarsia formosa Gahan (Burnett 1964) were in agreement with those predicted by the Nicholson-Bailey model. Under natural conditions, such population cycles are not common. Nicholson (1933) recognized this and suggested that the oscillations predicted by the model would be characteristic of subpopulations. The population cycles of the subpopulations would be out of phase with one another, so the effect of localized extinction of subpopulations would be masked when examining population dynamics of the entire population.

Hassell-Varley Model

Hassell and Varley (1969) modified the Nicholson-Bailey model by adding a density dependent component. They did this by assuming that the area of discovery, a, decreased with an increase in parasite or predator density. The relationship between the area of discovery and parasite or predator density was assumed to be linear on a log scale. In other words, log a = log Q - m log P, where Q is the quest constant, m is the mutual interference constant, and P is the parasite density. This relationship was consistent with data from several laboratory studies of parasite-host or predator-prey interactions (Huffaker and Kennett 1956, Burnett 1956a, 1956b, 1958, Ullyett 1949, 1949/1950). By substituting into the Nicholson-Bailey model, the Hassell-Varley model can be expressed as

$$N_{t+1} = \lambda N_t e^{-QP_t(1 - m)}$$

$$P_{t+1} = P_t(1 - e^{-QP_t(1 - m)})$$

where N_{t+1} is the number of hosts or prey at time t+1, λ is the rate of increase of the host, Q is the quest constant, P_t is the number of parasites or predators at time t, m is the mutual interference constant, and P_{t+1} is the number of parasites or predators at time t+1.

This model has 5 major assumptions. The first is that the number of encounters of parasites or predators influences the available searching time such that the mutual interference reduces the searching time in direct proportion to the frequency of encounters. The second assumption is that the searching efficiency decreases as

parasite density increases. The linear relationship between searching efficiency and parasite density resulting from these 2 assumptions is only an approximation because for some species, the relationship appears to be curvilinear (Varley et al. 1973). The third assumption is that the searching efficiency is not influenced by environmental factors other than parasite density. A variety of environmental factors such as temperature (Crocker et al. 1975, Frazer and Gilbert 1976), physical characteristics of the searching universe (Rabb and Bradley 1968, Elsey 1974, Murdoch and Oaten 1975, Belcher and Thurston 1982), and the spatial distribution of hosts or prey (Murdoch and Oaten 1975, Hassell 1978), has been shown to influence the searching efficiency of parasites or predators. The fourth assumption is that the rate of increase of the host or prey is constant (i.e., λ is a constant). The final assumption is that 1 parasitized host or a given number of prey consumed at time t produced 1 parasite or predator offspring at time t+1.

The Hassell-Varley model predicts population oscillations that are dampened by the mutual interference constant, m. Such cycles are characteristic of populations of parasites and hosts or predator and prey under laboratory conditions (Ullyett 1949, 1949/1950, Huffaker and Kennett 1956, Burnett 1956a, 1956b, 1958, Huffaker et al. 1963). Parasite-host and predator-prey populations appear to demonstrate similar cycles under field conditions (Broadhead and Cheke 1975, Ives 1976). However, the ability of the Hassell-Varley model to predict population numbers under field conditions cannot be assessed properly because the mutual interference constant, m, cannot be calculated directly from field

data and may be confounded with behavioral attributes of the parasite or predator and physical characteristics of the universe searched. To represent this complex process adequately in the model will require a decomposition of the single parameter, m, into several parameters. These parameters should attempt to describe the mutual interference among parasites or predators considering such factors as the searching efficiency of the parasite or predator and how it changes with changes in environmental conditions (e.g., temperature, prey density, heterogeneity of the universe searched, etc.), and the demonstration of functional and numerical responses by a parasite or predator population.

Numerous studies have been conducted to examine the effects of a variety of factors on the behavior of the Hassell-Varley model. Rogers (1972) examined the effect of random and non-random search and host distribution on the number of hosts attacked. Hassell and Rogers (1972) investigated the effect of host distribution, mutual interference, parasite aggregation, and prey density on the stability of the population oscillations. Interference and parasite aggregation and their effect on searching time were examined by Rogers and Hassell (1974). Beddington (1975) investigated the effects of interference and handling time on the searching efficiency of parasites or predators. Allen (1975) modified the model to extend through space as well as time.

The models just presented are elegant mathematical descriptions of predator-prey dynamics. All of these models are most useful for describing some 1 predator-1 prey interactions. Under field conditions, the interactions of predator and prey populations usually involve

a complex of predators feeding upon a variety of prey. Such interaction necessitates a more complex model of predation. Therefore, in response to this need, other researchers have formulated either empirical models of predation to describe interactions of a specific group of predators on 1 or more prey species or models of the attack behavior of arthropod predators. In the following, the predator-power and efficacy model, the Holling functional response model, and a model of coccinellid-aphid dynamics will be discussed.

The Predator-Power and Efficacy Model

Tamaki et al. (1974) formulated the predator-power and efficacy model in an attempt to predict the impact of an arthropod predator complex on a pest (prey) population. They were interested in predicting the impact of the predator complex, Orius tristicolor (White), Geocoris pallens, G. bullatus, Nabis americoferus, N. alternatus, Hippodamia convergens, Coccinella transversoguttata, and Chrysopa carnea Stephens, on the aphid pest (prey) complex, Myzus persicae, Macrosiphum euphorbiae (Thomas), and Aphis fabae Scopoli, in potatoes and sugar beets. To do this, they constructed a model modified from that proposed by Bombosch (1963 as cited in Tamaki et al. 1974). Their model is

$$A_{n+1} = (A_n - EK_n)q$$

where A_{n+1} is the prey density on day n+1, A_n is the prey density on day n, EK_n is the impact of the predator complex, and q is the rate of increase of the prey.

Estimates of all quantities, except the predator impact, were determined directly. The impact of the predator complex (EK_n)

was determined by estimating its 2 components, the predator efficacy (E) and the total predator power (K), separately. Predator efficacy (E), defined as the external factors such as temperature, seasonal variation, host density, and host plant, that affect predator power by reducing population densities of prey, was estimated by

$$E = \frac{A_0 q^n - A_n}{\sum_{j=1}^{n} K_j q^{n-j+1}}$$

where A_n and q are defined as before, A_0 is the prey density on day 0, and K_j is the predator power for species j. The predator power (K_j), defined as the number of prey consumed by predator species j, was estimated by

$$K_j = N_j C_j$$

where N_j is the density of predator species j, and C_j is the relative feeding capacity of predator species j. By assigning the predator species within a complex to a class based on feeding habits, the total predator power (K_n) was estimated by

$$K_n = \sum_{i=1}^{n} N_i C_i$$

where N_i and C_i are defined as before, except that their values refer to classes rather than species of predators.

Using their model, Tamaki et al. (1974) predicted the density of aphids in field plots of potatoes and sugar beets. They found reasonably good agreement of predicted and observed aphid densities. For some populations, however, the predicted and observed trends were not synchronous. The asynchrony was attributed to the effects of abiotic factors such as temperature and rain, and the effects of inter- and intraspecific competition on aphid populations.

Incorporation of some of these factors into the model was attempted by Tamaki and Long (1978). They added model structure to describe the effects of temperature on the rate of increase of the prey and the effects of temperature and prey density on predator feeding response. They found that the expanded model was somewhat better at predicting the impact of a predator complex on a prey population than the original model.

Cotton Pest Dynamics Models

The cotton pest dynamics models, MOTHZV-2 (Hartstack et al. 1976) and the Fye (1979) cotton model, were formulated to aid in the management of various cotton pests. The MOTHZV-2 model describes the dynamics of Heliothis zea, H. virescens, while the Fye model describes the dynamics of Pectinophora gossypiella, Lygus hesperus Knight, Trichoplusia ni, Bucculatrix thurberiella Busck, H. zea, and H. virescens. Both models are computer simulation models and contain subroutines to describe the mortality inflicted on pests by predators.

The predation subroutine of the MOTHZV-2 model calculates the mortality inflicted by some of the more common predator species found in Texas cotton. These include coccinellids, Collops spp., Orius spp., Geocoris spp., other hemipterous predators, Chrysopa spp., and spiders. The mortality inflicted on the prey (pest) population can either be set equal to a value determined from field estimates or calculated from equations that describe the probability of an individual prey being consumed. For the larval stage of the prey, the mortality estimates are adjusted for the age of the prey.

The predation subroutine in the Fye model calculates the mortality inflicted by a predator complex commonly found in Arizona cotton. The complex was composed of Nabis alternatus, N. americoferus, Geocoris punctipes (Say), G. pallens, Orius tristicolor, Zelus renardii Kolenati, Sinea confusa Caudell, Chrysopa carnea, Collops vittatus (Say), and Hippodamia convergens. This subroutine calculates the amount of mortality inflicted by a predator complex based on a series of predation indices that describe the feeding behavior of individual predator species. These indices were determined from laboratory studies.

These models incorporate relatively simple descriptions of predator activity. The simplicity is justified, however, in that these models were designed to forecast the time of occurrence of economically injurious levels of pest populations, and not to investigate the mechanisms associated with the process of predation. Such an investigation requires a more complex description of predation.

Holling Functional Response Model

The Holling functional response model describes the attack behavior of a predator species. This model was formulated in response to a field study in which Holling (1959b) found that the consumption of pine sawfly pupae, Neodiprion sertifer (Geoff.), by 3 rodents, Sorex cinereus cinereus Kerr, Blarina brevicauda talpoides Gapper, and Peromyscus maniculatus bairdii Hoy and Kennicott, increased with an increase in prey density. Holling (1959b) used the term, "functional response", as proposed by

Solomon (1949), to describe the change in number of prey consumed by an individual predator with changing prey density. From this experiment, Holling (1959b) defined 3 basic types of functional response curves, type I, II, and III. For the type I curve, the number of prey consumed per predator is directly proportional to the prey density. The type II curve describes a predator that increases its prey consumption at a continually decreasing rate. For the type III curve, the number of prey consumed per predator initially increases at an increasing rate, and at some inflection point, the number of prey consumed per predator increases at a decreasing rate.

To determine the general functional response model (type II), Holling (1959a) used an artificial predator-prey system consisting of sand paper discs as prey and blind-folded technician as the predator. Holling was able to derive an equation to describe the type II functional response by measuring the number of discs removed, the time spent searching for discs, the time required to remove a disc, and the initial density of discs. His basic equation called the "disc equation" is as follows:

$$Y = \frac{T_T ax}{1 + abx}$$

where Y is the number of discs removed, T_T is the total time ($T_T = T_S + bY$, where T_S is the time available for searching, and b is the time required to pick up 1 disc), a is the rate of searching multiplied by the probability of finding a disc in a fixed interval, T_T, and x is the density of the discs. This equation can be rearranged and expressed in a more general form as

$$N_a = N_t \left(1 - e^{-a'P_t(T - T_h(N_a/P_t))}\right)$$

where N_a is the number of prey consumed, N_t is the number of prey at time t, a' is the search rate of the predator, T_h is the handling time, and P_t is the number of predators at time t.

The Holling functional response model assumes that the total time available for searching and the handling time are constant. These assumptions appear to be valid for simple predator-prey systems.

Holling (1965) refined the type II equation to take into account 4 basic components of the predator response to prey density: rate of successful search, the time predators were exposed to prey, the time spent handling each prey, and hunger. The resulting equation (type III) is

$$N_a = N_t \left(1 - e^{\frac{-bP_t}{c}\left(T - \frac{T_h N_a}{P_t} - \frac{N_a}{bN_t P_t (N_t - N_a)}\right)}\right)$$

where N_a, N_t, P_t, and T_h are defined as above and a is the search rate of the predator ($bN_t/(1 + cN_t)$, where b and c are constants of nonlinear least squares regression). This model is based on the same assumptions as the type II model and has 1 additional assumption. This assumption is that the predator searching rate depends upon the number of prey available at any given moment.

The type I functional response model is a special case of the general or type II response (Holling 1965). The equation for the type I response is

$$N_a = N_t \left(1 - e^{-aTP_t}\right)$$

where N_a, N_t, T, and P_t are defined as above, and a is the instantaneous search rate. The assumptions of this model include constant search rate and searching lifetime, non-satiation of predators, and no influence of environmental factors on predation. These assumptions appear unrealistic, but could be rendered valid if the searching activity of a predator increased with increasing hunger (Holling 1965).

Murdoch and Oaten (1975) criticized Holling's analysis of functional response of predators because Holling did not consider the effects of spatial heterogeneity or prey patchiness shown by Huffaker (1958) and Huffaker et al. (1963) to be important. Murdoch and Oaten (1975) proposed a model of predator behavior such that a predator must spend time travelling between patches of prey in addition to other activities associated with predation. They also point out a number of mechanisms that can affect and stabilize predator-prey interactions. These include factors such as refuges for prey, spatial heterogeneity of habitat, an invulnerable class of prey, and patchiness of prey. An extensive discussion of the effect of and stability resulting from the mechanism and the mathematical proofs can be found in Murdoch and Oaten (1975), Oaten and Murdoch (1975a, 1975b, 1977), and Levin (1977).

Other studies have also demonstrated the importance of predator behavior on the functional response. Sandness and McMurtry (1970) demonstrated the effect of large densities of active prey on the functional response of predators. Murdoch and Oaten (1975), Oaten and Murdoch (1975b), and Akre and Johnson (1979) investigated the effect of predator switching from one prey type to an alternate

prey on the functional response. Thompson (1975) and Murdoch and Sih (1978) examined the effects of age structure in the prey consumption behavior of predators. Cook (1978) investigated the effect of predator preference on functional response.

Gutierrez et al. (1979) expanded the functional response model to a multipredator-multiprey model. Their model was patterned after the functional response model of Frazer and Gilbert (1976) that incorporated a function to describe the demand for prey by predators. The model by Gutierrez et al. (1979) is

$$(N_a)^k_{t+1} = N^k_t \sum_{i=1}^{n} \alpha_{ik} e^{-\sum_{j=1}^{m} \left[\frac{b_{jk} V_{jk} \beta_{ij} P^j_t T}{\alpha_{ik} N^k_t}\right]} (1 - e^{-a_{ijk} \alpha_{ik} N^k_t / b_{jk} V_{jk}})]$$

for j = 1,2,...,m, and i = 1,2,...,n, where N^k_t is the number of prey type k at time t, P^j_t is the number of predator type j at time t, α_{ik} is the proportion of prey type k in area i, β_{ij} is the proportion of predator type k in area i, b_{jk} is the maximum consumption of prey type k per predator of type j occurring in the time interval t to t+1, V_{jk} is the preference of predator type j for prey type k (this changes as population densities of all prey types change), and T is the change in time t. The coefficients, α_{ik}, β_{ij}, a_{ijk}, b_{jk}, and the prey preference index, V_{jk}, may be represented by complex functions. This model may be best suited to describe predator-prey interactions in the field because it attempts to describe many of the biological complexities found in multipredator-multiprey systems. However, the ease with which this model may be used is questionable due to the difficulties associated with quantifying some of the parameters of this model.

Coccinellid-Aphid Dynamics Model

The coccinellid-aphid dynamics model was the result of the combined efforts of 9 scientists who investigated the process of coccinellid (Coccinella californica Mannerheim and C. trifasciata Mulsant) predation on pea aphid (Acyrthosiphon pisum) populations in alfalfa (Baumgaertner et al. 1981). This model is an extension of the C. trifasciata-A. pisum dynamics model constructed by Frazer and Gilbert (1976). Like the Frazer and Gilbert model, the coccinellid-aphid dynamics model consists of a series of simultaneous equations that describe the dynamics of coccinellid and aphid populations based on prey and predator developmental rates, and the effects of prey and predator density, predator voracity, prey age distribution, temperature, predator reproduction and survival rates, and predator movement on predation rate (Baumgaertner et al. 1981). The simultaneous equations are solved using computer simulation.

The coccinellid-aphid dynamics model predicted within an order of magnitude the number of coccinellids required to best exploit aphid populations for maximum reproduction (Frazer et al. 1981). The discrepencies between predicted and observed numbers were due in part to the behavior of the coccinellids (Frazer et al. 1981). Their behavior also made estimation of their population densities very difficult (Ives 1981a). The predator population density was required to initialize the model.

The construction and analysis of the coccinellid-aphid model represents a thorough study of the dynamics of predator and prey populations. Such studies are necessary to understand predator-

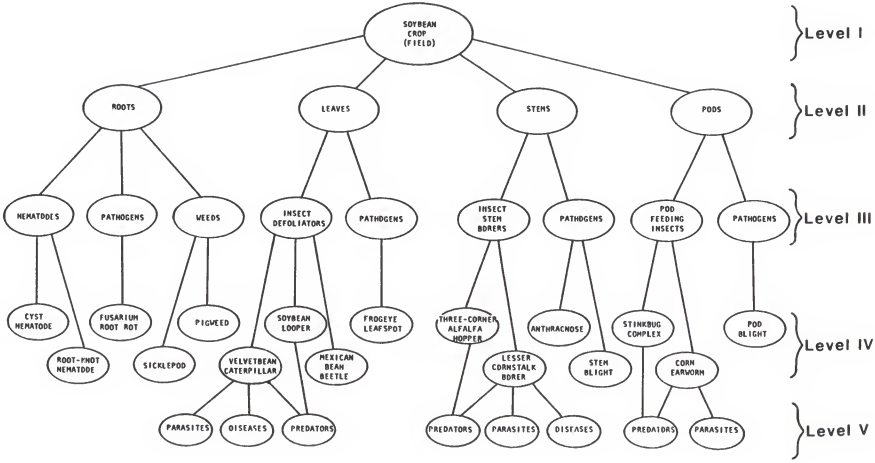
prey dynamics and to assess the regulative ability of a predator population. Study of the dynamics of one of the populations without similar study of the other can lead to the omission of factors that significantly affect the dynamics of both populations.

In this chapter, the models discussed described various aspects of predation by a single species or small group of predator species on a single prey species or small group of prey species. These models have limited utility in describing the predation activity of a complex of predators on the dynamics of numerous prey species within a system. Description of the activity of a predator complex within a system requires the construction of a multipredator-multiprey model. This model like that proposed by Gutierrez et al. (1979) must be complex because the process of predation is complex. However, the amount of complexity built into the model is limited by the number of parameters that can be estimated practically under field conditions. Such a compromise between complexity and practicality should result in a multipredator-multiprey model that describes predation, the process that links the dynamics of predator and prey populations.

At the University of Florida, researchers are attempting to construct a computer simulation model of the dynamics of populations of organisms found within the soybean agroecosystem as an aid to the development and analysis of pest management strategies. As can be seen from Figure 1, the dynamics of the populations are linked by developmental and trophic processes. At present, the developmental processes of the soybean plant and VBC have been modeled. However, many of the trophic processes remain to be modeled,

Figure 1. A conceptual model of the Florida soybean agroecosystem.

SOYBEAN CROP/PEST COMPLEX



including arthropod predation on various pest species (Level V, Figure 1). To make the task of modeling arthropod predation in the soybean agroecosystem tractable, it was decided that predation by an indigenous complex on a single pest should be investigated and modeled first. VBC was chosen as the pest species because of the economic damage it can inflict and because considerable information about VBC already had been collected and incorporated into the model.

The multipredator-VBC model could not be patterned after any of the empirical models presented in this review because of the large number of potential predator species (about 120, Whitcomb, unpublished data)[1] of VBC occurring within the soybean agroecosystem. Therefore, the initial model of VBC predation was constructed to describe the patterns of mortality for each life stage based on an index of predator density.

Such a description required knowledge of the stage specific mortality inflicted by the predator complex, the species responsible for the mortality, and the densities of the populations of key predator species within the complex. Methods for obtaining this information (reviewed in the previous chapter) were virtually non-existent, except for the methods used by Ashby (1974) and McDaniel and Sterling (1982). Therefore, the purpose of my study was to devise a method to provide the information required by the initial model of arthropod predation on VBC eggs and larvae.

Note

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ESTIMATION OF RATES OF ARTHROPOD PREDATION ON SMALL AND MEDIUM VELVETBEAN CATERPILLAR LARVAE, 1980

Introduction

Specific estimates of the mortality imposed on each life stage of VBC are required for the construction of a VBC population dynamics model (Stimac and Barfield 1979). These estimates must quantitatively express patterns of total mortality and the mortality attributable to each group of natural enemies that includes arthropod predators (Stimac and O'Neil 1982). Quantitative espression of patterns of arthropod predation requires estimates of the mortality attributable to the key predator species comprising the complex under field conditions (Stimac and O'Neil 1982). These patterns of total and predator-induced mortality may be discerned by the simultaneous use of mark-release-recapture of prey and direct observation techniques. Using the mark-release-recapture technique, one can obtain estimates of total prey mortality, the mortality inflicted by predators, and the mortality inflicted by factors other than predators. By the use of the direct observation technique, the predator-induced mortality estimate can then be partitioned into the mortality inflicted by key predator species. This bilevel partitioning of the total mortality estimates results in a quantitative estimate of the rate of arthropod predation for each predator species.

In 1980, the method was used to estimate rates of arthropod predation on small (first and second instar; length < 12.5 mm) and medium (third and fourth instar; length 12.5-25 mm) VBC larvae. Experiments were conducted on these life stages because arthropod predators were thought to have their greatest impact on VBC dynamics through the mortality they inflict on these life stages. The use of these stages, therefore, should provide an adequate test of the utility of the method for estimating rates of arthropod predation on immature life stages of VBC. In addition, small and medium larvae were chosen for the experiments because initial estimates of total mortality for small larvae and the efficiency of the sampling device used in recapturing both small and medium larvae had been determined previously (Luna 1979, Luna et al. 1982).

Materials and Methods

The objective of this study was to devise a method for quantitative estimation of rates of arthropod predation in soybean fields and to use this method to estimate rates for small and medium VBC larvae. To achieve this objective, experiments were conducted each week in which estimates of total mortality and non-predator-induced mortality were obtained from mark-release-recapture of prey studies. At the same time, the key predator species responsible for the mortality were identified from direct observation studies. In addition to the above information, the predator complex within the field was characterized with weekly estimates of the densities of arthropod predators species and/or functional groups.

Rates of arthropod predation were estimated in 2 soybean fields, a 1-ha plot at Green Acres Agronomy Farm near Gainesville, Florida (Green Acres site), and a 4-ha commercial field, west of Archer, Florida (Archer site). Two fields were used so that rates of predation and predator complexes at each site could be compared.

Experiments were conducted from 30 June-22 September 1980 at the Green Acres site on Bragg variety soybeans planted with a 76 cm row spacing. The beans were planted in 3 June with a pre-plant application of 1774.4 ml/ha oryzalin and 591.5 ml/ha metribuzin herbicides. At the Archer site, experiments were conducted from 2 July-27 August 1980 on Hardee variety soybeans planted with a 91 cm row spacing. These beans were planted on 13 May and treated pre-plant with 4731.8 ml/ha alachlor herbicide. The Archer site was also treated with methomyl on 16 August to suppress populations of noctuid larvae. On the day the experiments were conducted, the phenological stage of the plants was determined using the criteria set forth by Fehr et al. (1971). Canopy temperature readings were taken every 2 hours in 1 of 2 ways: thermocouple probes connected to an Esterline Angus® Model PD2064 microprocessor at Green Acres, and a psychrometer at Archer.

Mark-Release-Recapture Technique

Laboratory reared larvae used in the releases made at Green Acres were marked with either radioactive phosphorus (^{32}P) or Calco Oil Red dye® (American Cyanamid) by allowing them to feed 36-48 hours on 200 grams of artificial diet (Greene et al. 1976) containing either 2.5 ml of 5 μCi/ml ^{32}P solution or 0.5 grams of

Calco Oil Red dye. The larvae released at Archer were marked by allowing them to feed 36-48 hours on 200 grams of artificial diet to which had been added 0.5 grams of Calco Oil Red dye. Radioactive phosphorus could not be used at the Archer site because the site did not meet federal standards for introduction of radioactive materials in the environment.

Estimates of the total mortality were obtained by releasing 20 marked larvae onto the foliage in 91 cm of row at 2 randomly chosen sites within the field. At each site, a series of releases was made. These releases were spaced at successive 3 m intervals down the row. At Green Acres, the series was composed of 4 releases: a release of small larvae marked with red dye, a release of small larvae marked with ^{32}P, a release of medium larvae marked with red dye, and a release of medium larvae marked with ^{32}P. At Archer, the series was composed of 2 releases: a release of small larvae marked with red dye, and a release of medium larvae marked with red dye. Prior to a release of larvae, the foliage at a release site was shaken to remove indigenous larvae. The release sites were sampled 24 hours after a release by using a modified clam trap that was 80% and 89% efficient at recovering small and medium larvae, respectively (Luna et al. 1982). The losses due to dispersal out of the release site were considered negligible because Luna (1979) found that small larvae do not readily disperse out of a 91 cm row area within 24 hours after a release. Medium larvae were assumed to behave similarly to small larvae.

In each field, releases were made into a field cage in an attempt to estimate mortality induced by factors other than predators.

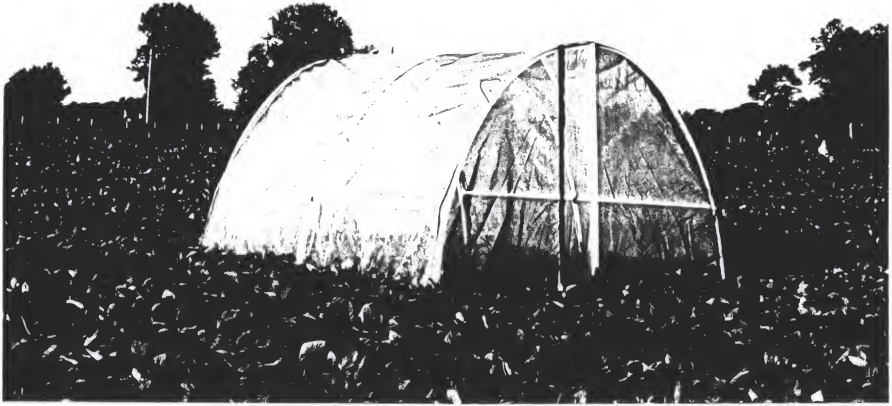
The mortality of larvae released in a field cage will be referred to as background mortality. The field cages were quonset type (3.05 m X 3.05 m X 2.26 m; Figure 2) and designed to exclude as many predators as possible. Two days prior to a release, the foliage within a cage was vacuumed with a D-Vac® sampler. One release, consisting of 20 marked larvae released onto the foliage in 91 cm of row, was made within a cage each week for each stage and for each marking technique. The release sites within the cage were sampled 24 hours after a release by harvesting the plants and returning them to the laboratory where the foliage was carefully searched for larvae.

The presence of the ^{32}P marker was determined by the use of a gas flow windowless proportional counter. The presence of the dye was determined by dissecting larvae under 10 X magnification. If present, the dye was concentrated in the fat body and prosternal gland.

Direct Observation Technique

Direct observation studies, modified from that proposed by Whitcomb (1967b), were conducted concurrently with the mark-release-recapture study. Observations were made at 20 stations set up in a circular configuration across the field. Each station consisted of 3 leaves located in the canopy foliage in 91 cm of row. A total of 10 larvae was placed at a station. At 15 stations, only 1 size class of larvae was placed on the foliage (10 stations had small larvae, and 5 stations had medium larvae). At each of the remaining stations, 5 small and 5 medium larvae were placed

Figure 2. Large field cage used in the estimation of background mortality.



on the foliage. An observer moved from station to station and recorded any predation events observed. A predation event was defined as the successful capture of 1 prey item by an arthropod predator(s). Before leaving a station, the observer would replace any missing larvae. The 20 stations at Green Acres site were observed from 6 am–6 pm and 7 pm–9 pm, and were also checked once at midnight and at 5 am on the following day. Night observations were made using a headlight with a red filter. At the Archer site, the stations were observed from 6 am–6 pm.

Estimates of Predator Population Densities

The relative densities of predator populations within each field were sampled each week by means of a shake cloth. The samples were taken on the same day as the mark-release-recapture of prey and direct observation studies were conducted. A sample was taken by beating the foliage in 91 cm of row onto a shake cloth spread on the ground between the rows (Luna et al. 1982). The dislodged predators were identified to the lowest appropriate taxon and the number in each taxon recorded. Five random samples were taken between 10 am and 1 pm within the Green Acres field. At the Archer site, 8 samples were taken between 10 am and 3 pm by systematic sampling with a random start.

Results and Discussion

Initial Partitioning of Total Mortality

During the season at Green Acres, the mean daily total mortality of larvae marked with ^{32}P and released within the field

varied from 55-100% for small larvae (Table 5 and Figure 3) and from 51.7 - 82.5% for medium larvae (Table 5 and Figure 4). The mean daily total mortality of larvae marked with red dye varied from 40-100% for small larvae (Table 6 and Figure 3) and from 36.7-80% for medium larvae (Table 6 and Figure 4). The background mortality indicated by the mortality of larvae marked with ^{32}P and released within the field cage varied from 45-100% for small larvae (Table 5 and Figure 3) and from 25-95% for medium larvae (Table 5 and Figure 4). The background mortality estimates for red dye marked larvae had a range of 40-95% for small larvae (Table 6 and Figure 3) and 13.3-100% for medium larvae (Table 6 and Figure 4). On some sample dates, the daily background mortality was as great or greater than the total mortality. This was due in part to the inability of the field cage to exclude predators that spent a majority of the time on the soil surface (ground predators). Therefore, the daily background mortality estimates may have been inflated due to mortality inflicted by ground predators that were not excluded by the field cages. For the present, the effect of the presence of ground predators on the mortality inflicted on larvae released within the field cage is assumed to be negligible because the magnitude of this effect cannot be determined from these experiments.

During the period of September 8-22, soybean plants at the Green Acres site suffered nearly complete defoliation as a result of a large population of indigenous noctuid larvae. The daily mortality estimates of VBC larvae from September 8-22 (Figures 3 and 4), therefore, may have been influenced by resource depletion.

Table 5. The percent mean daily mortality estimates and the estimates of mortality induced by all predators for small and medium velvetbean caterpillar larvae marked with ^{32}P at Green Acres, 1980. The field suffered 95-98% defoliation from September 8-September 22.

Date, Phenological Stage[a], and Height	Field Released (Total)		Within Field Cage (Background)		Predator-Induced Mortality[b]	
	Small (SD)	Medium (SD)	Small (SD)	Medium (SD)	Small (SD)	Medium (SD)
June 30 V5, 35 cm	72.5 (24.8)	62.5 (24.8)	50	40	22.5	22.5
July 7 V5-6, 43 cm	65 (14.1)	75 (7.1)	45	65	20	10
July 14 V7-8, 61.5 cm	55 (-)	65 (-)	70	60	0[c]	5
July 21 V8, R1, 68 cm	80 (-)	62.5 (3.5)	70	25	10	37.5
July 28 V10, R1, 72 cm	60 (-)	57.5 (3.5)	50	25	10	32.5
August 4 V15, R2, 100 cm	92.5 (10.6)	67.5 (3.5)	80	40	12.5	27.5
August 11 V14, R2, 106 cm	64.2 (13.0)	51.7 (2.4)	53.3	53.3	10.8	0[c]

Table 5. continued.

Date, Phenological Stage[a], and Height	Field Released (Total)		Within Field Cage (Background)		Predator-Induced Mortality[b]	
	Small (SD)	Medium (SD)	Small	Medium	Small	Medium
August 18 V15, R2, 120 cm	83.3 (4.7)	56.7 (23.6)	86.7	46.7	0[c]	10
August 25 V15, R3, 118 cm	95 (7.1)	65 (7.1)	70	90	25	0[c]
September 1 V15, R3, 110 cm	100 (-)	76.7 (9.4)	93.3	80	6.7	0[c]
September 8 V15, R4, 113 cm	100 (-)	60 (14.1)	100	90	0	0[c]
September 15 V15, R4-5, 113 cm	97.5 (3.5)	82.5 (10.6)	100	95	0[c]	0[c]
September 22 V15, R5-6, 112 cm	100 (-)	65 (7.1)	100	90	0	0[c]

[a]Phenological stages determined using the criteria set forth by Fehr et al. (1971).

[b]Predator-Induced Mortality = Total - Background

[c]Value set equal to zero because background mortality exceeded total mortality.

Figure 3. Patterns of percent daily total, background, and predator-induced mortality for small velvetbean caterpillar larvae released at Green Acres, 1980. The field suffered 95-98% defoliation from September 8-September 22.

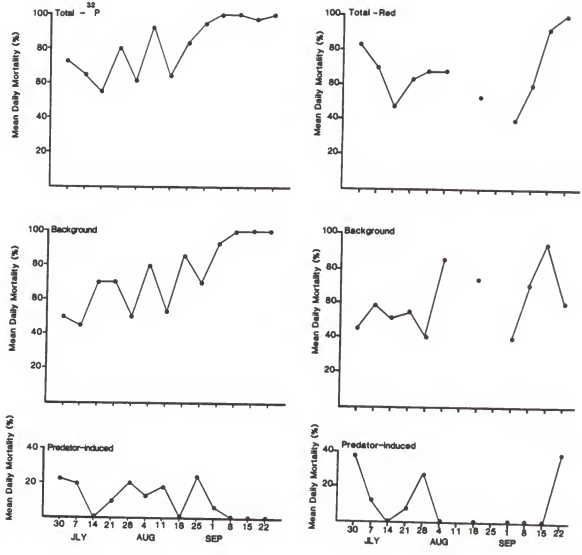

Total - ^{32}P
Total - Red
Background
Background
Predator-induced
Predator-induced
Mean Daily Mortality (%)
100
80
60
40
20
30 7 14 21 28 4 11 18 25 1 8 15 22
JLY
AUG
SEP

Table 6. The percent mean daily mortality estimates and the estimates of predator-induced mortality for small and medium velvetbean caterpillar larvae marked with Calco Oil Red dye at Green Acres, 1980. The field suffered 95-98% defoliation from September 8-September 22.

Date, Phenological Stage[a], and Height	Field Release (Total) Small (SD)	Field Release (Total) Medium (SD)	Within Field Cage (Background) Small (SD)	Within Field Cage (Background) Medium (SD)	Predator-Induced Mortality[b] Small (SD)	Predator-Induced Mortality[b] Medium (SD)
June 30 V5, 35 cm	82.5 (3.5)	67.5 (10.6)	45	40	37.5	27.5
July 7 V5-6, 43 cm	70 (28.3)	70.6 (15.0)	58.8	-[c]	11.2	-[c]
July 14 V7-8, 61.5 cm	47.5 (10.6)	67.5 (24.8)	50	45	0[d]	22.5
July 21 V8, R1, 68 cm	62.5 (3.5)	60 (7.1)	55	25	7.5	35
July 28 V10, R1, 72 cm	67.5 (24.8)	47.5 (3.5)	40	40	27.5	7.5
August 4 V15, R2, 100 cm	67.5 (3.5)	45 (35.4)	85	65	0[d]	0[d]
August 11[c] V14, R2, 106 cm	-	-	-	-	-	-
August 18 V15, R2, 120 cm	53.3 (-)	36.7 (42.4)	73.3	80	0[d]	0[d]

Table 6. continued.

Date, Phenological Stage[a], and Height	Field Released (Total) Small (SD)	Field Released (Total) Medium (SD)	Within Field Cage (Background) Small	Within Field Cage (Background) Medium	Predator-Induced Mortality[b] Small	Predator-Induced Mortality[b] Medium
August 25[c] V15, R3, 118 cm	-	-	-	-	-	-
September 1 V15, R3, 110 cm	40 (18.9)	73.3 (-)	40	13.3	0	60
September 8 V15, R4, 113 cm	60 (-)	80 (7.1)	70	80	0[d]	0
September 15 V15, R4-5, 113 cm	92.5 (3.5)	80 (7.1)	95	85	0[d]	0[d]
September 22 V15, R5-6, 112 cm	100 (-)	60 (14.1)	60	100	40	0[d]

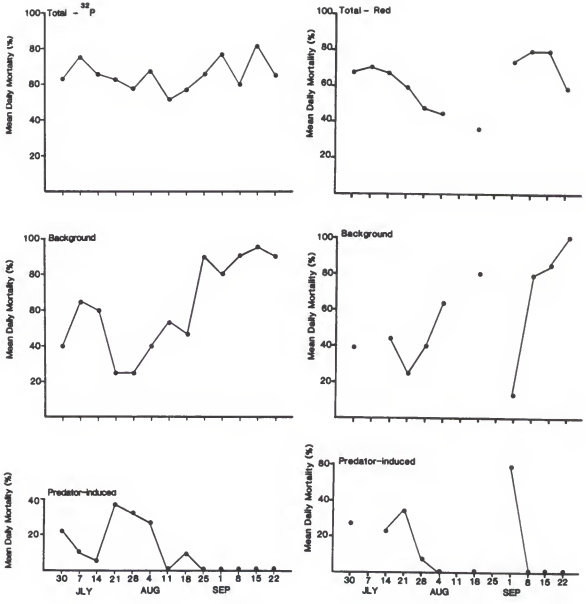
[a]Phenological stage determined using criteria set forth by Fehr et al. (1971).

[b]Predator-Induced Mortality = Total - Background

[c]Insufficient number of larvae for release.

[d]Values set equal to zero because background mortality exceeded total mortality.

Figure 4. Patterns of the percent daily total, background, and predator-induced mortality for medium velvetbean caterpillar larvae released at Green Acres, 1980. The field suffered 95-98% defoliation from September 8-September 22.


Total - ^{32}P
Total - Red
Background
Background
Predator-induced
Predator-induced
Mean Daily Mortality (%)
100
80
60
40
20
30 7 14 21 28 4 11 18 25 1 8 15 22
JLY
AUG
SEP

At Green Acres, the mortality estimates of larvae marked with ^{32}P were more reliable than those from larvae marked with red dye. The larvae marked with ^{32}P could be identified more objectively than those marked with red dye because the red dye could not be distinguished from red pigments found in the dark form of VBC that occurs in abundance late in the season. Consequently, comparisons of mortality estimates between sites were made using the estimates obtained from larvae marked with ^{32}P.

At the Archer site, the mean daily estimates of total mortality of larvae released in the field varied from 47.5-90% for small larvae (Table 7 and Figure 5) and from 25-72.5% for medium larvae (Table 7 and Figure 6). Variability of total larval mortality estimates may have been influenced by the presence or absence of imported fire ants, Solenopsis invicta Buren, at a site where larvae were released. No effort was made to avoid placing a release site near a fire ant nest. Estimates of daily background mortality varied from 50-85% for small larvae (Table 7 and Figure 5) and 0-95% for medium larvae (Table 7 and Figure 6). Detection of the dye was not a problem with larvae released at the Archer site because experiments were terminated before the dark form of VBC larvae became abundant in the field.

As in the Green Acres field, estimates of daily background mortality, on some sample dates, were greater than estimates of total mortality (Figures 5 and 6). Fire ants were the main cause of high daily background mortality. The presence of the ants within the cage resulted from the inability of the cage to exclude

Table 7. The percent mean daily mortality estimates and the estimates of the predator-induced mortality for small and medium velvetbean caterpillar larvae released at Archer, 1980. The field was sprayed on August 16 with methomyl.

Date, Phenological Stage[a], and Height	Field Released (Total)		Within Field Cage (Background)		Predator-Induced Mortality[b]	
	Small (SD)	Medium (SD)	Small	Medium	Small	Medium
July 2 V6, 37 cm	90 (-)	72.5 (38.9)	80	25	10	47.5
July 9 V7, 44 cm	75	37.5	85	45	0[c]	0[c]
July 16 V7-8, 61.5 cm	72.5 (17.7)	65 (28.3)	55	95[d]	17.5	0[c]
July 23 V9, 76 cm	80 (7.1)	72.5 (17.7)	70	0	10	72.5
July 30 V11, 83 cm	75 (-)	25 (14.1)	85	45	0[c]	0[c]
August 6 V14, 107 cm	47.5 (10.6)	30 (21.2)	60	35	12.5	0[c]

Table 7. continued.

Date, Phenological Stage[a], and Height	Field Released (Total) Small (SD)	Field Released (Total) Medium (SD)	Within Field Cage (Background) Small	Within Field Cage (Background) Medium	Predator-Induced Mortality[b] Small	Predator-Induced Mortality[b] Medium
August 13 V16, R2, 104 cm	86.7 (9.4)	63.3 (14.1)	66.7	20	20	43.3
August 20 V15-16, R2, 115cm	68.3 (25.9)	36.7 (23.6)	70	80	0[c]	0[c]
August 27 V15-16, R3-4, 111 cm	55 (7.1)	35 (21.2)	50	30	5	5

[a]Phenological stage determined using criteria set forth by Fehr et al. (1971).

[b]Predator-Induced Mortality = Total - Background

[c]Values set equal to zero because background mortality exceeded total mortality.

[d]Imported fire ants at release site.

Figure 5. Patterns of the percent daily total, background, and predator-induced mortality for small velvetbean caterpillar larvae released at Archer, 1980. The field was sprayed August 16 with methomyl.

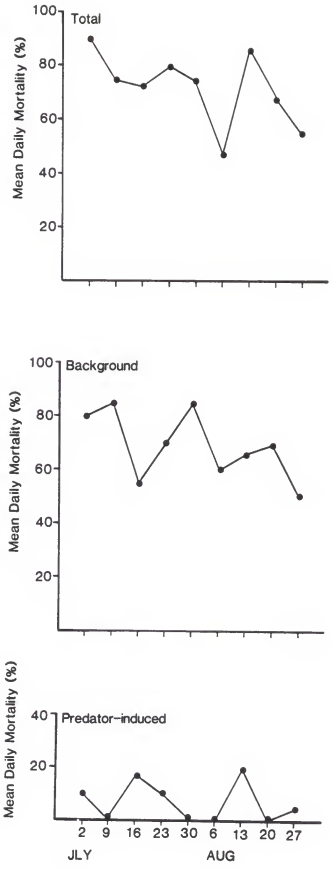
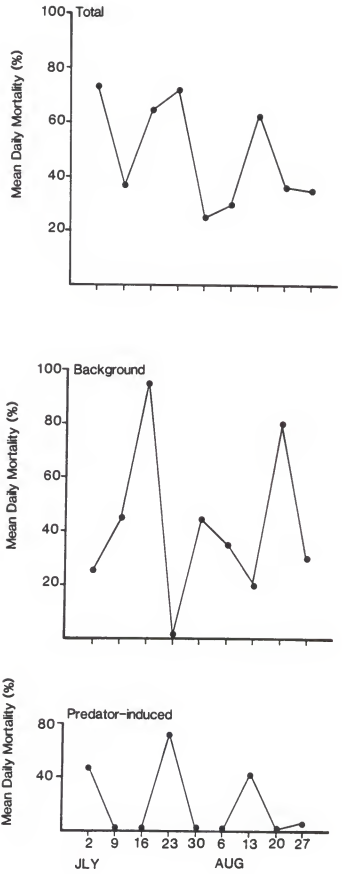

Total
Mean Daily Mortality (%)
100
80
60
40
20
Background
Mean Daily Mortality (%)
100
80
60
40
20
Predator-induced
Mean Daily Mortality (%)
40
20
2 9 16 23 30 6 13 20 27
JLY
AUG

Figure 6. Patterns of the percent daily total, background, and predator-induced mortality for medium velvetbean caterpillar larvae released at Archer, 1980. The field was sprayed on August 16 with methomyl.


Total
Mean Daily Mortality (%)
100
80
60
40
20
Background
Mean Daily Mortality (%)
100
80
60
40
20
Predator-induced
Mean Daily Mortality (%)
80
40
2
9
16
23
30
6
13
20
27
JLY
AUG

fire ants and the impracticality of searching the field for an ant-free location for cage placement. To control fire ants, Amdro® bait was applied to the soil surface within the cage and around the outside perimeter of the cage. This attempt, however, was unsuccessful.

Mortality inflicted by all predators can be estimated by the difference between total mortality and background mortality assuming that none of the background mortality was due to predation. Estimates of mortality inflicted by all predators was set equal to zero for all dates on which background mortality exceeded total mortality. At the Green Acres site, estimates of daily mortality inflicted by all predators ranged from 0-25% for the small larvae marked with ^{32}P (Table 5 and Figure 3) and from 0-37% for medium larvae marked with ^{32}P (Table 5 and Figure 4). Estimates of daily predator-induced mortality ranged from 0-40% for small red dye marked larvae (Table 6 and Figure 3) and from 0-60% for medium red dye marked larvae (Table 6 and Figure 4). The range of predator-induced mortality estimates for larvae released at the Archer site was 0-20% per day for small larvae (Table 7 and Figure 5) and 0-72.5% per day for medium larvae (Table 7 and Figure 6).

The seasonal average rates of arthropod predation at Green Acres and Archer were 13.8% per day for small larvae and 28.5% per day for medium larvae. Assuming that these rates of mortality, determined at 1 prey density, are representative of the rates imposed on the range of prey densities that occur within the field and that these rates are imposed every day during the development of small and medium larvae (7 days, Reid 1975), only 17 individuals

of a cohort of 100 newly emerged larvae would survive to the end of the medium stage. This represents an 83% reduction in the density of VBC larvae by the end of the fourth instar.

Partitioning of Predator-Induced Mortality by Species

The direct observation study allows the daily predator-induced mortality estimates to be partitioned according to predator species if one assumes that the seasonal average proportion of prey observed to be consumed in 1 day represents the proportion of prey consumed each day by a predator species. This assumption is reasonable because the daily estimates of the densities of predators did not vary dramatically from week to week (predator densities discussed later in text). Results are expressed as the ratio of the total number of times a given predator species was observed consuming a prey over the entire season to the total number of predation events observed over the entire season. The partitioning of the predator-induced mortality estimates according to predator species could not be done because of the small number of predation events recorded in each field. Instead, the results from direct observation were used to identify those species that could be considered as the major contributors to predation mortality.

A total of 70 predation events, 36 for small larvae and 34 for medium larvae, was observed in the Green Acres field. Nymphs of the nabid, Tropiconabis capsiformis (Germar), were observed to consume the greatest proportion of small larvae (27.8%, Table 8). For medium larvae, nymphs and adults of the nabid, Nabis roseipennis Reuter, were observed to consume the greatest

Table 8. The seasonal average proportion of velvetbean caterpillar larvae preyed upon by a given predator species as determined by direct observation at Green Acres, 1980. (Total observations = 70).

Predator species	Proportion consumed
SMALL LARVAE (total = 36)	
Tropiconabis capsiformis (Germar) nymphs	0.28
Geocoris punctipes (Say) nymphs and adults	0.19
Theridion albidum Banks adult	0.11
Hentzia palmarum (Hentz)	0.08
Nabis roseipennis Reuter nymphs and adults	0.08
Misumenops spp.	0.06
Chiracanthium spp.	0.06
Tettigoniidae	0.06
Podisus maculiventris (Say) nymphs	0.06
Labidura riparia (Pallas) nymph	0.03
MEDIUM LARVAE (total = 34)	
Nabis roseipennis Reuter nymphs and adults	0.18
Misumenops spp.	0.15
Labidura riparia (Pallas) nymphs and adults	0.15
Peucetia viridans (Hentz)	0.09
Calleida decora (F.) larvae and adults	0.09
Chiracanthium spp.	0.09
Geocoris punctipes (Say) adults	0.06
Hentzia palmarum (Hentz)	0.03
Tettigoniidae	0.03
Tropiconabis capsiformis (Germar) nymphs	0.03
Podisus maculiventris (Say) nymphs	0.03

Table 8. continued.

Predator species	Proportion consumed
Tetragnathus spp.	0.03
Oxyopes salticus Hentz	0.03
Theridion albidum Banks	0.03

proportion (11.8% for adults and 5.9% for nymphs; Table 8). These results are consistent with the work of others who also found that nabids consume relatively large proportion of immature stages of noctuid pests of soybeans (Buschman et al. 1977a, Richman et al. 1980, Gardner et al. 1981). At the Archer site, 53 predation events were recorded, 12 for small larvae and 41 for medium larvae. The imported fire ant was observed to consume the greatest proportion of small (75%; Table 9) and medium (87.5%; Table 9) larvae.

Most observations of predation were recorded between 6 am-6 pm with a peak between 10 am-2 pm at Green Acres (Table 10) and between 8 am-noon at Archer (Table 11). Differences in the peak times of observation may have been due in part to the schedule for making observations within the 2 fields. The observation schedule at Green Acres was more rigorous than that for Archer. Some of the differences in the peak times of observation also may have been attributable to the behavior of individual predator species because for some species, foraging periodicity was apparent (Table 10-11).

Temperature may have also played a role in determining peak times of predation events. Most observations were recorded at mean canopy temperatures between 23-32°C at Green Acres (Table 12, while those at Archer were recorded at mean ambient temperatures between 25-32°C (Table 13). At Green Acres, soybean canopy temperatures rarely exceeded 32°C in the afternoon, and canopy temperatures less than 23°C were usually recorded between 10 am-6am. At Archer, ambient temperatures usually exceeded 32°C

Table 9. The seasonal average proportion of velvetbean caterpillar larvae preyed upon by a given predator species as determined by direct observation at Archer, 1980. (Total observations = 53).

Predator species	Proportion consumed
SMALL LARVAE (total = 12)	
Solenopsis invicta Buren	0.75
Conomyrma spp. (black form)	0.17
Hentzia spp.	0.08
MEDIUM LARVAE (total = 41)	
Solenopsis invicta Buren	0.88
Conomyrma spp.	0.02
Tettigoniidae	0.02
Oxyopes spp.	0.02
Chiracanthium inclusum (Hentz)	0.02
Clubionidae[a]	0.02

[a]Spider immature - not identifiable to genus.

Table 10. The percent of predation events by each predator species within each time interval for small and medium velvetbean caterpillar larvae at Green Acres, 1980.

Predator spcies	Time of Day					
	6:00am–10:00am	10:01am–2:00pm	2:01pm–6:00pm	6:01pm–10:00pm	10:01pm–2:00am	4:00am–6:00am
Total	25.7	30	28.6	5.7	7.1	2.9
Tropiconabis capsiformis (Germar)	4.3	7.1	4.3	0	0	0
Nabis roseipennis Reuter	2.9	1.4	5.7	1.4	1.4	0
Geocoris punctipes (Say)	1.4	5.7	5.7	0	0	0
Misumenops spp.	1.4	4.3	1.4	0	2.9	0
Theridion albidum Banks	7.1	1.4	0	0	0	0
Labidura riparia (Pallas)	4.3	2.9	1.4	1.4	0	0
Hentzia palmarum (Hentz)	1.4	2.9	1.4	1.4	0	0
Peucetia viridans (Hentz)	1.4	0	0	0	0	0
Chiracanthium spp.	0	0	0	0	2.9	2.9
Tettigoniidae	0	0	4.3	0	0	0
Calleida decora (F.)	0	1.4	2.9	0	0	0
Podisus maculiventris (Say)	1.4	1.4	0	1.4	0	0
Tetragnathus spp.	0	1.4	0	0	0	0
Oxyopes salticus Hentz	0	0	1.4	0	0	0

Table 11. The percent of predation events by each predator species within each time interval for small and medium velvetbean caterpillar larvae at Archer, 1980.

Predator species	Time of Day					
	6:00am–8:00am	8:01am–10:00am	10:01am–noon	12:01pm–2:00pm	2:01pm–4:00pm	4:01pm–6:00pm
Total	1.9	32.1	28.3	13.2	11.3	13.2
Solenopsis invicta Buren	0	28.3	24.5	9.4	9.4	11.3
Conomyrma spp. (black form)	0	1.9	3.8	1.9	0	0
Hentzia palmarum (Hentz)	0	1.9	0	0	0	0
Chiracanthium spp.	1.9	0	0	0	1.9	0
Tettigoniidae	0	0	0	0	0	1.9
Oxyopes salticus Hentz	0	0	0	1.9	0	0

Table 12. The percent of predation events by each predator species on small and medium velvetbean caterpillar larvae within a temperature interval at Green Acres, 1980. Some species are not listed due to a lack of temperature information.

Predator species	Temperature (°C)				
	20 - 21	23 - 27	29 - 32	33 - 35	36 - 38
Total	8.5	27.1	39	10.2	11.8
Tropiconabis capsiformis (Germar)	3.3	0	11.9	1.7	1.7
Nabis roseipennis Reuter	0	3.4	8.5	0	3.4
Geocoris punctipes (Say)	0	0	6.8	5.1	1.7
Misumenops spp.	0	1.7	0	0	0
Theridion albidum Banks	1.7	6.8	0	0	0
Labidura riparia (Pallas)	0	1.7	1.7	0	1.7
Hentzia palmarum (Hentz)	0	3.4	1.7	0	1.7
Peucetia viridans (Hentz)	0	1.7	1.7	1.7	0
Chiracanthium spp.	1.7	6.8	0	0	0
Tettigoniidae	0	0	1.7	0	1.7
Calleida decora (F.)	0	0	0	1.7	3.4
Podisus maculiventris (Say)	1.7	1.7	1.7	0	0
Tetragnathus spp.	0	0	1.7	0	0
Oxyopes salticus Hentz	0	0	1.7	0	0

Table 13. The percent of predation events by each predator species on small and medium velvetbean caterpillar larvae within each temperature interval at Archer, 1980. Some species are not listed due to a lack of temperature information.

Predator species	Temperature (°C)				
	25 - 26	27 - 28	29 - 30	31 - 32	> 33
Total	43.2	11.4	15.9	22.7	6.8
Solenopsis invicta Buren	43.2	11.4	11.4	20.5	6.8
Conomyrma spp. (black form)	0	0	4.5	0	0
Oxyopes salticus Hentz	0	0	0	2.3	0

from about 1:30 pm until 5 pm (temperature data for both fields summarized in Appendix A). Soil temperatures probably reached daily minima and maxima at approximately the same time of day as canopy temperatures. Imported fire ants, as ground dwelling predators, may have been responding to the soil temperatures rather than canopy temperatures. However, because no instruments were available to measure soil temperature, no comparisons can be made.

The patterns of mortality found in each field may have been influenced by the cultivar of soybeans planted within the field. The cultivars used in the experiments differed in maturity groups (Bragg = Group VII; Hardee = Group VIII), and because of this, their growth characteristics (i.e., acquisition of leaf area, period of bloom, etc.) differed (Hinson and Smith 1969). Such cultivar differences may influence the composition of the arthropod predator complex within a field, as has been demonstrated for several cultivars of cotton (Shepard et al. 1972, Schuster et al. 1976, Henneberry et al. 1977, Agnew et al. 1982). Comparisons of the composition of the predator complexes from the Green Acres and Archer fields revealed few differences (Table 14). The patterns of VBC larval mortality in each field were also similar (Figures 3-6). This suggests that the cultivar differences in soybeans had little or no effect on the pattern of VBC larval mortality. To assess the effect of cultivar differences on patterns of mortality properly, however, more rigorous testing will be required.

Comparisons of the predation by each species (Table 8 and 9) suggest that imported fire ants, when present, dominated the

Table 14. The mean relative densities (variance) of predator populations at Green Acres (GA) and Archer (AR), 1980.

Date	Total	Clubionidae	Thomisidae	*Peucetia viridans* (H.)	Salticidae	*Oxyopes salticus* H.	Small Spiders	Lycosidae	Other Spiders	Formicidae	Carabidae
June 30 - July 2											
GA	1.2 (1.3)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
AR	1.3 (2.8)	0.1 (0.1)	0 (-)	0 (-)	0 (-)	0 (-)	0.5 (0.6)	0 (-)	0 (-)	0 (-)	0 (-)
July 7 - July 9											
GA	1.8 (1.1)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0 (-)	0 (-)	0 (-)	0 (-)
AR	2.5 (1.4)	0.3 (0.2)	0.3 (0.2)	0 (-)	0 (-)	0 (-)	0.5 (0.6)	0 (-)	0 (-)	0.6 (0.8)	0 (-)
July 14 - July 16											
GA	1.6 (3.3)	0 (-)	0.2 (0.2)	0.4 (0.8)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0 (-)
AR	2.8 (2.5)	0.3 (0.2)	0 (-)	0 (-)	0 (-)	0 (-)	0.4 (0.3)	0 (-)	0 (-)	0.8 (1.4)	0.1 (0.1)
July 21 - July 23											
GA	2.2 (3.7)	0 (-)	0.2 (0.2)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.6 (0.3)	0.2 (0.2)	0 (-)
AR	----------						Rain			----------	
July 28 - July 30											
GA	3.4 (4.3)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.6 (0.8)	0 (-)	0 (-)	0.8 (1.2)	0 (-)
AR	3.9 (2.7)	0 (-)	0 (-)	0.3 (0.3)	0.3 (0.3)	0 (-)	0.8 (0.9)	0 (-)	0.3 (0.3)	1.5 (1.7)	0 (-)

Coccinellidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Oecanthus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus (Reuter)	Reduviidae
0.2	0	0.6	0	0	0	0.4	0	0	0	0
(0.2)	(-)	(0.8)	(-)	(-)	(-)	(0.8)	(-)	(-)	(-)	(-)
0	0	0	0	0.1	0	0	0	0	0.5	0
(-)	(-)	(-)	(-)	(0.1)	(-)	(-)	(-)	(-)	(0.6)	(-)
0	0	0.6	0	0	0	0	0	0	1.0	0
(-)	(-)	(0.3)	(-)	(-)	(-)	(-)	(-)	(-)	(1.0)	(-)
0	0	0.3	0	0	0	0	0	0	0.6	0
(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)	(0.6)	(-)
0	0	0.4	0	0	0	0.2	0	0.2	0	0
(-)	(-)	(0.8)	(-)	(-)	(-)	(0.2)	(-)	(0.2)	(-)	(-)
0	0	1.1	0	0	0	0	0	0	0.1	0
(-)	(-)	(0.7)	(-)	(-)	(-)	(-)	(-)	(-)	(0.1)	(-)
0	0	0.8	0	0	0.2	0	0	0	0	0
(-)	(-)	(0.7)	(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)
					Rain					
0	0	1.8	0	0	0	0	0	0.2	0	0
(-)	(-)	(0.7)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)	(-)
0	0.3	1.5	0	0	0	0	0	0.3	0.8	0.3
(-)	(0.3)	(1.7)	(-)	(-)	(-)	(-)	(-)	(0.3)	(2.3)	(0.3)

Table 14. continued.

Date	Total	Clubionidae	Thomisidae	Peucetia viridans (H.)	Salticidae	Oxyopes salticus H.	Small Spiders	Lycosidae	Other Spiders	Formicidae	Carabidae
August 4 - August 6											
GA	7.6 (110.3)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0 (-)	0 (-)	0.6 (1.8)	0 (-)
AR	6.0 (5.4)	0.5 (0.6)	0 (-)	0 (-)	0.1 (0.1)	0 (-)	0.8 (0.8)	0 (-)	0.3 (0.2)	1.9 (0.7)	0.1 (0.1)
August 11 - August 13											
GA	9.4 (5.8)	0.2 (0.2)	0.6 (0.3)	0 (-)	0 (-)	0 (-)	1.0 (1.0)	0 (-)	0 (-)	0.4 (0.3)	0.6 (0.3)
AR	6.5 (50.7)	0.1 (0.1)	0 (-)	0 (-)	0 (-)	0 (-)	0.3 (0.2)	0 (-)	0 (-)	4.5 (48.3)	0 (-)
August 18 - August 20											
GA	3.2 (2.7)	0 (-)	0.4 (0.3)	0 (-)	0 (-)	0 (-)	0.4 (0.3)	0 (-)	0.2 (0.2)	0.2 (0.2)	0 (-)
AR	2.9 (3.2)	0.3 (0.2)	0.3 (0.2)	0 (-)	0 (-)	0 (-)	0.1 (0.1)	0.3 (0.2)	0.1 (0.1)	1.1 (1.8)	0 (-)
August 25 - August 27											
GA	7.2 (3.2)	0 (-)	0.4 (0.8)	0 (-)	0 (-)	0 (-)	1.4 (1.3)	0 (-)	0 (-)	0.4 (0.3)	0 (-)
AR	10.4 (47.2)	0 (-)	0.1 (0.1)	0 (-)	0.1 (0.1)	0 (-)	1.1 (1)	0 (-)	0.3 (0.5)	6 (43.7)	0 (-)
September 2											
GA	12 (16)	0.2 (0.2)	0.2 (0.2)	0 (-)	0 (-)	0 (-)	2.0 (1.5)	0.4 (0.3)	0.2 (0.2)	0 (-)	0.2 (0.2)
September 8											
GA	12.8 (54.7)	0.2 (0.2)	0.6 (0.8)	0.2 (0.2)	0.2 (0.2)	1.6 (2.8)	0 (-)	0 (-)	0 (-)	0.6 (1.8)	0 (-)

Coccinellidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Oecanthus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus (Reuter)	Reduviidae
0	0	0.8	0	0.6	0	0	4.6	0.6	0.2	0
(-)	(-)	(0.7)	(-)	(0.8)	(-)	(-)	(105.8)	(0.3)	(0.2)	(-)
0	0.4	1.0	0	0.5	0	0	0	0.7	0	0.5
(-)	(0.3)	(1.1)	(-)	(1.1)	(-)	(-)	(-)	(0.8)	(-)	(1.1)
0	0.4	3.2	0	0.2	0	0	1.4	0.6	0	1.0
(-)	(0.3)	(2.2)	(-)	(0.2)	(-)	(-)	(2.8)	(0.8)	(-)	(1.0)
0	0.1	0.8	0	0	0	0	0	0.4	0.3	0.1
(-)	(0.1)	(0.9)	(-)	(-)	(-)	(-)	(-)	(0.4)	(0.5)	(0.1)
0	0.2	0.6	0	0	0.2	0	0.2	0	0.2	0.6
(-)	(0.2)	(0.8)	(-)	(-)	(0.2)	(-)	(0.2)	(-)	(0.2)	(1.8)
0	0.3	0.5	0	0	0	0	0	0	0	0
(-)	(0.2)	(0.3)	(-)	(-)	(-)	(-)	(-)	(-)	(-)	(-)
1.0	0.4	1.0	0	0.2	0	0	0	1.4	0	1.0
(1.5)	(0.3)	(1.0)	(-)	(0.2)	(-)	(-)	(-)	(0.3)	(-)	(1.5)
0	0.1	1.8	0	0	0.1	0	0	0.5	0.1	0.1
(-)	(0.1)	(0.9)	(-)	(-)	(0.1)	(-)	(-)	(0.3)	(0.1)	(0.1)
0.6	0.6	2.4	0.4	0.8	0.6	0	0	3.2	0	0.2
(0.8)	(0.8)	(3.8)	(0.8)	(1.7)	(0.8)	(-)	(-)	(0.7)	(-)	(0.2)
0.4	1.4	4.2	0	0.4	0	0	0.2	2.6	0	0
(0.3)	(3.8)	(7.2)	(-)	(0.8)	(-)	(-)	(0.2)	(13.3)	(-)	(-)

Table 14. continued.

Date	Total	Clubionidae	Thomisidae	Peucetia viridans (H.)	Salticidae	Oxyopes salticus H.	Small Spiders	Lycosidae	Other Spiders	Formicidae	Carabidae
September 15											
GA	6.0 (10.6)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.4 (0.3)	0.2 (0.2)	0 (-)	0 (-)
September 22											
GA	8.8 (22.7)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	1.4 (0.3)	0 (-)	0 (-)	0 (-)	0 (-)

Coccinellidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Oecanthus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus (Reuter)	Reduviidae
0 (-)	1.0 (1.0)	3.4 (4.8)	0 (-)	0.4 (0.3)	0 (-)	0 (-)	0 (-)	1.0 (1.5)	0 (-)	0 (-)
1.4 (0.8)	0.4 (0.8)	3.4 (9.3)	0 (-)	0.8 (0.7)	0 (-)	0.6 (1.8)	0 (-)	0.8 (0.7)	0 (-)	0 (-)

predation on VBC larvae. Their dominance, however, did not appear to extend to the species composition of the predator complex because the densities of the species comprising the complexes within the 2 fields were similar (Table 14). To determine if the addition of imported fire ants to the complex resulted in differences in the rates of mortality, comparisons of the estimates of daily total mortality were made using a 2-way ANOVA procedure with location and weeks as factors. No differences in the rates of daily total mortality for small and medium larvae could be detected between the 2 fields (small: $F_{1,8df} = 0.05$, $P > 0.10$; medium: $F_{1,8df} = 3.76$, $0.1 > P > 0.05$) or among weeks (small: $F_{8,8df} = 0.20$, $P > 0.10$; medium: $F_{8,8df} = 0.79$, $P > 0.10$). Daily background mortality estimates were also similar (Figures 3 - 6). This suggests that imported fire ants inhibit the foraging activity of other predator species, yet compensate for this inhibition by inflicting comparable amounts of mortality on a pest population. Imported fire ants also have been shown to play a similar role in the dynamics of Heliothis virescens in Texas cotton (Sterling et al. 1979, Agnew et al. 1982). In general terms, the results of this study and those done in Texas cotton suggest that the mortality inflicted upon prey populations is not necessarily dependent upon the presence or absence of a particular species within the complex. The species comprising the complex may be able to compensate for one another in terms of the mortality they inflict upon a prey population. The generality of such an effect, however, must be the subject of further study.

In conclusion, the proposed method for quantifying arthropod predation did not allow the partitioning of total mortality estimates into predator-induced and non-predator-induced components, and the identification of the major predator species responsible for the predator-induced mortality. The estimates of the seasonal average predation mortality, determined from the use of the method, were 13.8% per day for small larvae and 28.5% per day for medium larvae. The majority of this mortality was attributable to nabids and imported fire ants at Green Acres and Archer, respectively. These mortality estimates and key predator species may not be representative of the predation activity occurring within the field because of the lack of consideration of the action of ground dwelling predators (ground predators). Some modifications of the method will be required to separate background mortality from ground predator mortality and to characterize the role of ground predators in the mortality inflicted on VBC populations.

ESTIMATION OF RATES OF ARTHROPOD PREDATION ON VELVETBEAN CATERPILLAR EGGS AND LARVAE, 1981 AND 1982

Introduction

The experiments conducted in 1980, in addition to demonstrating the utility of the 2-step method for partitioning estimates of total mortality, revealed that the arthropod predators inflicting mortality on VBC larvae were not found exclusively on the foliage of the soybean plant. Ground dwelling predators could also inflict significant mortality. This was seen in the mortality estimates of larvae released in the large field cages used in 1980 to estimate background mortality. VBC larvae were also exposed to attack on the ground because at times, their violent defensive behavior resulted in the larvae falling to the ground. The amount of the mortality inflicted by ground dwelling predators was dependent upon the frequency with which these predators searched the foliage for prey, the frequency with which VBC larvae fell to the ground, and the frequency with which VBC larvae returned to the plant after falling.

In 1981 and 1982, rates of arthropod predation by both foliage and ground dwelling predators were estimated for immature life stages of VBC. Experiments were conducted with VBC eggs and larvae to determine the general applicability of the method for

partitioning estimates of total mortality. In 1982, only small VBC larvae were used in the experiments in an attempt to refine estimates of rates of arthropod predation.

Materials and Methods

To estimate rates of arthropod predation by foliage and ground predators requires a trilevel partitioning of total mortality estimates. Such partitioning can be accomplished by the simultaneous use of mark-release-recapture of prey and direct observation techniques. At the first level of partitioning, mortality induced by all predators can be separated from non-predator-induced mortality by subtracting background mortality from total mortality. The predator-induced mortality can then be further partitioned according to the position in the habitat occupied by the predator (ground or foliage). This is done by subtracting the mortality due to predators on the ground from the mortality due to all predators. Finally, the amount of mortality attributable to each predator species can be assigned using the information obtained from the direct observation study.

In addition to the partitioning, the 3 frequencies associated with mortality due to ground predators must be estimated. The frequency with which ground predators searched the foliage for prey can be inferred from the direct observation study. The frequency of fall of VBC larvae can be estimated directly. The frequency with which VBC larvae returned to the plant after falling was not estimated, but was assumed to be very low.

The relative densities of the predator species within the field were also estimated in order to determine the species composition of the predator complex.

In 1981 and 1982, rates of arthropod predation on immature VBC were estimated on Bragg variety soybeans planted at Green Acres Agronomy Farm. In 1981, VBC eggs, and small, medium, and large (fifth and sixth instar; length > 25 mm) larvae were used in the experiments that were conducted from 30 June until 29 September. The soybeans were planted 12 June with a 76 cm row spacing and a pre-plant application of 295.7 ml/ha trifluralin and 887.2 ml/ha metribuzin.

In 1982, small VBC larvae were used in the experiments that were conducted 6 July through 14 September. The soybeans were planted 9 June with a 76 cm row spacing and a pre-plant application of 1182.8 ml/ha trifluralin and 887.2 ml/ha metribuzin.

On each day the experiments were conducted in 1981 and 1982, plant height was measured and the phenological stage of the plants was determined using the criteria set forth by Fehr et al. (1971). Upper, middle, and lower canopy temperatures, and soil temperatures (ca. 12.5 mm below the soil surface) were measured and recorded by means of thermocouples connected to an Esterline Angus® PD 2064 microprocessor.

Mark-Release-Recapture Technique

1981. For each release, unmarked VBC eggs (ca. 12-24 hours old) from a laboratory culture were attached to the underside of leaflets with UCAR 152® adhesive (Union Carbide). One egg was placed

on each leaflet, and the leaf containing the eggs was marked with flagging tape tied around its rachis. The adhesive was assumed not to affect the behavior of arthropod predators because it had been shown to have no effect on the behavior of parasitic insects (W. J. Lewis, personal communication)[1]. The laboratory reared larvae used in the releases were marked with ^{32}P using the same procedure as in 1980.

The density of eggs, and small, medium, and large larvae released each week varied from 5-10 over the season. The density of each stage was varied in an attempt to reduce the possible attractiveness of artificially high densities of prey at a release site.

Rates of daily total mortality of eggs and larvae were estimated each week at 3 randomly chosen sites within the field. At each site, a series of 3 releases was made. The release sites within a series were spaced at successive 3 m intervals down the row. At the first site in the series, a known density of eggs and small larvae was released. Known densities of medium and large larvae were released at the second and third series sites, respectively. A release site within a series consisted of the foliage in 91 cm of row. Prior to a release, the plants at a site were shaken to remove indigenous larvae. Each site was sampled 24 hours after a release. Leaves onto which eggs had been attached were collected and returned to the laboratory for examination. Larvae were recaptured using a sheet arena sampler (described in Luna et al. 1982).

Daily rates of mortality inflicted by ground predators were estimated by means of releases of known densities of eggs and larvae made at 3 sites within a large field cage, identical to that used in 1980 (Figure 2). The estimates of mortality obtained from these releases will be referred to as estimates of large field cage mortality. Each release site within the field cage consisted of the foliage in 91 cm of row. On the day before a release, the large field cage was swept using a 38 cm sweep net to remove foliage dwelling predators. Each site within the cage was sampled 24 hours after a release. The leaves containing eggs were collected and returned to the laboratory. For the larvae, plants at a site were shaken over a standard shake cloth. The plants were shaken twice to insure the removal of all remaining larvae.

Estimates of daily background mortality were obtained by releasing known numbers of eggs and larvae within 2 small field cages placed randomly within the field. The small field cage fit over the plants in 91 cm of row (Figure 7). The plants contained within the cage were shaken twice to remove predators and/or prey before being placed within the cage. The bases of the plants were treated with Tac-Trap® to prohibit the entry of ground predators. Eggs and all stages of larvae were released within a cage. The plants within a cage were sampled 24 hours after a release. The leaves containing eggs were collected and returned to the laboratory for examination. To recapture the larvae within a cage, the plants were beaten against the side

Figure 7. The small field cage used to estimate the background mortality in 1981 and 1982.

of the cage and the dislodged larvae collected. The inside of the cage and the remaining plants were then carefully searched for any remaining larvae.

Upon returning to the laboratory, the leaves onto which the eggs were attached were examined under 10X magnification, and the condition of each egg recorded. The larvae recaptured at each release site were frozen, and the presence of the ^{32}P marker was determined using a gas flow windowless proportional counter as previously described. Missing immatures were assumed to have succumbed.

Some missing eggs may have been due to egg hatch because newly emerged VBC larvae usually consume the remains of the chorion shortly after hatching (Watson 1916). To determine the number of missing eggs due to egg hatch on each release date beginning 21 July, a known number of eggs was placed in a sealed petri dish and held in the insectary at Green Acres for the duration of a release (24 hours). The number of eggs hatching in that period was recorded.

During the last 4 weeks of the season, additional releases of eggs dusted with scales from the wings of VBC moths (dusted eggs) were made onto the row adjacent to a regular egg release site. This was done to investigate in a preliminary way the effect of the procedures for collecting eggs from moths in a laboratory culture on rates of mortality. Dusting eggs with moth wing scales was chosen as the way to make eggs from a laboratory culture more like field-laid eggs because in a related species,

Heliothis zea, the moth scales were the source of a kairomone that stimulated a host seeking response from Trichogramma evanescens Westwood, the major egg parasitoid of H. zea (Lewis et al. 1972). It was assumed that if VBC had such a kairomone that its source would also be in the moth scales. It was further assumed that arthropod predators would respond to a kairomone, if present, in a similar way as T. evanescens.

1982. The rates of total, large field cage, and background mortality of small larvae were estimated using essentially the same procedures as those used in 1981. The larval marking scheme, the range of densities of larvae released at a site, and the larval recapture method for field and large field cage releases were the same as those used in 1981. The number of releases made to estimate each mortality component (total, large field cage, and background), however, was increased to 5 releases. This was done in an attempt to reduce the variability associated with the mortality estimates.

The recovery procedure of larvae placed in small field cages was also modified. To recover the larvae, the stems of plants within a cage were cut near the soil surface. The plants were then pulled inside the cage where they were shaken to dislodge small larvae. The foliage and the inside of the cage were then carefully searched and the larvae were collected.

The frequency with which small VBC larvae fell to the ground was determined at 4 stations placed within the observation circle. At each of these stations, the frequency of fall was estimated by means of a trap composed of 2 shallow aluminum pans (43 cm

X 31 cm) that were secured about the base of the plants (Figure 8). The shallow pans were filled with ethylene glycol to a depth of approximately 12 mm. The day prior to trap placement, the foliage at a trap site, the foliage adjacent to the site on the same row, and the foliage on adjacent rows were shaken onto a shake cloth to remove indigenous larvae. The day traps were placed in the field, the foliage at a site was shaken again to insure the removel of indigenous larvae. After traps were in place, 10 small larvae were placed on 5 leaves in the foliage above each trap. Each leaf was marked with flagging tape tied to its rachis. Two larvae were placed on each leaf. After placement, the leaf was held motionless for 5 seconds so that the larvae could establish a foothold. During each round of observation, the traps used for estimating frequency of fall were checked. The number of larvae that had fallen into a trap was recorded, and the dead larvae were removed from the trap. Before leaving a trap, an observer would replace any missing or dead larvae.

At each frequency of fall station, the width of the canopy and the length of row within the trap were measured each week. This was done to determine the ground area served by a trap. Estimates of the mean leaf are per plant were obtained from R. J. O'Neil[2].

Direct Observation

1981. The direct observation study was conducted concurrently with the mark-release-recapture of prey study. Observations were made of the predation events occurring on both the foliage and on the ground. Predation events were observed at 20 foliage stations

Figure 8. The traps used to estimate the frequency of fall of small velvetbean caterpillar larvae in 1982.

and 6 ground stations arranged in 2 circles that sat side by side. After 1 September, the number of stations was reduced to 20 foliage and 4 ground stations contained within 1 circle, due to the loss of observers with the beginning of fall semester.

Foliage observation stations consisted of 3 plants located in 91 cm of row. Known densities of eggs and larvae were released on 3 leaves, 1 leaf on each plant, marked with flagging tape tied around their rachises. Only 1 life stage of VBC was placed at a station. One observer moved from station to station and recorded any predation events observed. A predation event was defined as the successful capture of 1 prey item by an arthropod predator(s). Predators consuming prey were identified to the lowest appropriate taxon either in the field, or the predator was collected and identified in the laboratory. Before leaving a station, an observer would replace any missing immatures.

The density of VBC immatures placed at a station, varied over the season. The minimum density of eggs, and small and medium larvae placed at a station was 5 individuals, and for the large larvae, 3 individuals. The maximum density of eggs, and small and medium larvae was 10 individuals, and for the large larvae, 5 individuals. Stations in both circles were run at minimum density on 7 July and 14 July. On 21 July and 28 July, 1 circle was run at minimum density, and the other at maximum density to compare the effects of prey density on the occurrence of predation events. Both circles were run at maximum density from 4 August through 1 September. After 1 September, the 2 circles were reduced to 1 circle that was run at maximum density.

Ground observation stations consisted of the area between 2 rows and extended 91 cm down the row. Upon arrival at a ground station, an observer placed 1 small, 1 medium, and 1 large larva on the ground and observed them for 10 minutes during the daytime observation period (8 am–6 pm) and for 5 minutes during the night observation period (6 pm–8 am). Any predation events were recorded. A ground predation event was defined as the successful capture of 1 prey item by 1 or more predators. Unsuccessful attacks were also recorded. Predators preying upon the larvae were identified in the same manner as for the foliage observations. Any larva preyed upon during an observation period was replaced.

From 30 June to 1 September, 2 observers worked simultaneously in the field from 8 am–6 pm with 1 observer in each circle. After 1 September, the observations stations were condensed into 1 circle that was manned by 1 observer. One observer checked all stations from 7 pm–9 pm, midnight–2 am, and 5 am–7 am on the following day. Night observations were made using a headlight with a red filter.

Beginning 15 September, eggs dusted with wing scales from VBC moths were placed with non-dusted eggs at egg stations. Three dusted eggs were placed with 7 non-dusted eggs at each egg station. The leaf onto which the dusted eggs were placed was chosen arbitrarily.

1982. The direct observation study was conducted concurrently with the mark-release-recapture of prey study. The procedures for directly observing predation events on small larvae were similar to those used in 1981. Observations were made at 20 foliage and

4 ground stations arranged in a circular configuration across the field. The density of larvae placed at a foliage station, did not vary over the season, but remained constant at 10 individuals per station. At the ground stations, 3 small larvae were placed on the ground and observed for 10 minutes.

A continuous sequence of observations were made at all stations within the circle by 1 observer from 6 am-8 am. This shorter time interval was chosen based on the results of the observation studies conducted in 1980 and 1981.

Estimating Predator Population Density

1981. Population densities of foliage predators were estimated each week by means of shake cloth samples at 5 randomly chosen sites within the field. The samples were taken on the same day as the mark-release-recapture of prey and direct observation studies were conducted. Predator populations were sampled at 3 times of day: 9 am-10 am, 2 pm-3 pm, and 6 pm-7 pm. Each sample consisted of shaking the foliage in 91 cm of row over a shake cloth (Luna et al. 1982). Predators were identified to the lowest appropriate taxon and the number in each taxon recorded.

Densities and activities of ground predator populations were estimated by means of 20 pitfall traps (MacFadyen 1962). The location of each trap within the field was determined by first dividing the field into 4 equal sized quadrats. Five random locations within each quadrat were then established for trap placement. This was done to insure that the densities of ground predator populations were sampled over the entire field. The pitfall traps consisted of 473.2 ml jars that were buried in the

soil, so that the lip of the jar was level with the soil surface. Each trap was half filled with ethylene glycol. The pitfall traps were placed in the field on the same day as the mark-release-recapture of prey and direct observation studies were conducted. The traps were removed 24 hours later.

1982. The densities of arthropod predator populations were estimated each week by means of 5 shake cloth samples taken at random within the field. Samples consisted of shaking the foliage in 91 cm of row (Luna et al. 1982). Dislodged predators were identified to the lowest appropriate taxon and the number in each taxon recorded. Samples were taken at 10 am-11 am and at 3 pm-4 pm on the same day as the mark-release-recapture of prey and direct observation studies were conducted.

Results and Discussion

Partitioning of Total Mortality

In 1981, the rates of mean daily total mortality inflicted upon VBC eggs and larvae varied over the season. Estimates of total mortality had a range of 36.7-90% for eggs, 33.3-100% for small larvae, 30-80% for medium larvae, and 40-100% for large larvae (Tables 15-18 and Figures 9-12). Mortality estimates for those immatures released within the large field cage (large field cage mortality) varied from 30-90% for eggs, 35-100% for small larvae, 10-90% for medium larvae, and 0-100% for large larvae (Tables 15-18 and Figures 9-12). Background mortality estimates had a range of 20-55% for eggs, 20-90% for small larvae,

Table 15. The percent mean daily mortality estimates for velvetbean caterpillar eggs at Green Acres, 1981.

Date,[a] Stage, and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
July 7 V2-3, 27 cm	5	53.3 (29.8)	90 (22.4)	35 (33.5)	18.3	55	0[d]
July 14 V3-4, 43 cm	5	46.7 (53.8)	30 (67.1)	20 (44.7)	26.7	10	16.7
July 21 V5-6, 63 cm	10	36.7 (27.9)	50 (63.3)	35 (15.8)	1.7	15	0[d]
July 28 V7-8, R1-2, 70 cm	10	73.3 (38.6)	70 --	35 (47.4)	38.3	35	3.3
August 4 V11-12, R2, 77 cm	10	76.6 (10.5)	80 (31.6)	40 (31.6)	36.7	40	0[d]
August 11 V11-13, R2, 90 cm	10	80 (31.6)	65 (15.8)	35 (47.4)	45	30	15
August 18 V11-13, R3-4, 90 cm	10	66.7 (27.9)	60 (31.6)	50 --	16.7	10	6.7
August 25 V11-13, R5, 93 cm	10	70 (18.3)	45 (15.8)	45 (47.4)	25	0	25

Table 15. continued.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
September 1 V11-13, R5-6, 98 cm	10	36.7 (10.5)	45 (15.8)	30 (47.4)	6.7	15	0[d]
September 8 V11-13, R5-6, 100 cm	10	66.7 (17.9)	60 --	40 --	26.7	20	6.7
September 15 V11-13, R6, 101 cm	10	70 (36.5)	90 (15.8)	95 (47.4)	15	40	0[d]
September 22 V11-13, R6, 102 cm	10	50 (31.6)	50 (31.6)	25 (15.8)	25	25	0
September 29 V11-13, R6, 101 cm	10	90 --	NA[e]	65 (79.1)	25	NA	NA

[a]Phenological stage determined from criteria set forth by Fehr et al. (1971).

[b]Total: releases = 3; Large field cage: releases = 2; Background: releases = 2

[c]Predator-induced = Total - Background; Ground = Large field cage - Background; Foliage = Predator-induced - Ground

[d]Negative values (by calculation) set equal to zero.

[e]No releases made within the large field cage.

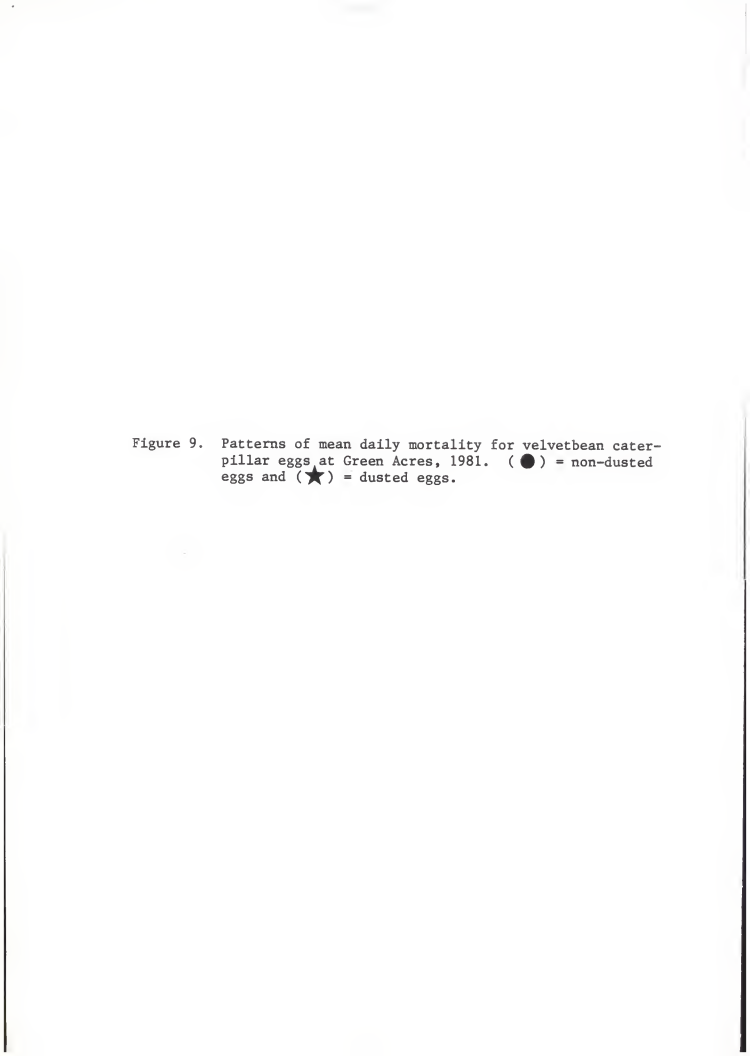


Figure 9. Patterns of mean daily mortality for velvetbean caterpillar eggs at Green Acres, 1981. (●) = non-dusted eggs and (★) = dusted eggs.

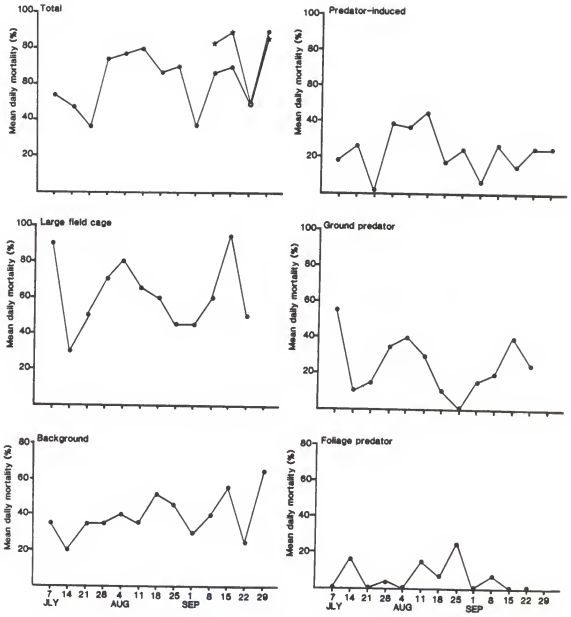

Total
Predator-induced
Large field cage
Ground predator
Background
Foliage predator
Mean daily mortality (%)
100
80
60
40
20
7 14 21 28 4 11 18 25 1 8 15 22 29
JLY
AUG
SEP

Table 16. The mean daily mortality estimates for small velvetbean caterpillar larvae at Green Acres, 1981.

Date,[a] Stage, and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
July 7 V2-3, 27 cm	5	73.3 (11.6)	60 --	20 (28.6)	53.3	40	13.3
July 14 V3-4, 43 cm	5	100 ---	50 (14.1)	70 (14.1)	30	0[d]	30
July 21 V5-6, 63 cm	10	55 (8.7)	60 --	35 (35.4)	20	25	0[d]
July 28 V7-8, R1-2, 70 cm	10	70 (26.5)	50 (14.1)	30 (14.1)	40	20	20
August 4 V11-12, R2, 77 cm	10	73.3 (20.8)	35 (7.1)	55 (21.2)	18.3	0[d]	18.3
August 11 V11-13, R2, 90 cm	10	96.7 (5.8)	85 (21.2)	60 (28.3)	36.7	25	11.7
August 18 V11-13, R3-4, 90 cm	10	33.3 (5.8)	60 (14.1)	40 --	0[d]	20	0[d]
August 25 V11-13, R5, 93 cm	10	100 ---	95 (7.1)	90 --	10	5	5
September 1 V11-13, R5-6, 98 cm	10	43.3 (15.3)	55 (7.1)	40 (42.4)	3.3	15	0[d]

Table 16. continued.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
September 8 V11-13, R5-6, 100 cm	10	43.3 (11.6)	65 (7.1)	40 (14.1)	3.3	25	0[d]
September 15 V11-13, R6, 101 cm	7	----------	----------	RAINED OUT	----------	----------	----------
September 22 V11-13, R6, 102 cm	10	43.3 (5.8)	55 (7.1)	55 (7.1)	0[d]	0	0[d]
September 29 V11-13, R6, 101 cm	10	40 (20.0)	NA[e]	30 (14.1)	10	NA	NA

[a]Phenological stage determined from criteria set forth in Fehr et al. (1971).

[b]Total: releases = 3; Large field cage: releases = 2; Background: releases = 2

[c]Predator-induced = Total - Background; Ground = Large field cage - Background; Foliage = Predator-induced - Ground

[d]All negative values (by calculation) set equal to zero.

[e]No releases made within the large field cage.

Figure 10. Patterns of mean daily mortality for small velvetbean caterpillar larvae at Green Acres, 1981.

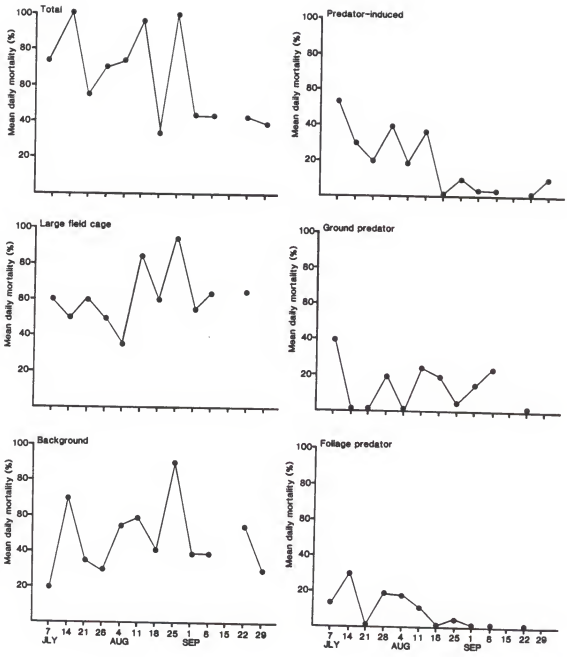

Total
Predator-induced
Large field cage
Ground predator
Background
Foliage predator
Mean daily mortality (%)
100
80
60
40
20
7 14 21 28 4 11 18 25 1 8 15 22 29
JLY
AUG
SEP

Table 17. The percent mean daily mortality estimates for medium velvetbean caterpillar larvae at Green Acres, 1981.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
July 7 V2-3, 27 cm	5	80 (34.6)	20 --	50 (14.1)	30	0[d]	30
July 14 V3-4, 43 cm	5	73.3 (11.6)	90 (14.1)	80 (28.3)	0[d]	10	0[d]
July 21 V5-6, 63 cm	10	46.7 (15.3)	40 --	20 (28.3)	26.7	20	6.7
July 28 V7-8, R1-2, 70 cm	10	53.3 (5.7)	30 --	25 (21.2)	28.3	5	23.3
August 4 V11-12, R2, 77 cm	10	30 (5.8)	40 --	20 (14.1)	0	10	0[d]
August 11 V11-13, R2, 90 cm	10	76.7 (25.2)	65 (7.1)	15 (7.1)	61.7	50	11.7
August 18 V11-13, R3-4, 90 cm	10	56.7 (15.3)	50 (28.3)	35 (7.1)	21.7	15	6.7
August 25 V11-13, R5, 93 cm	10	43.3 (11.6)	50 --	30 (7.1)	13.3	20	0[d]
September 1 V11-13, R5-6, 98 cm	10	36.7 (23.1)	45 (21.2)	10 --	26.7	35	0[d]

Table 17. continued.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
September 8 V11-13, R5-6, 100 cm	10	30 --	50 --	15 (21.2)	15	35	0[d]
September 15 V11-13, R6, 101 cm	10	---------- RAINED OUT ----------					
September 22 V11-13, R6, 102 cm	10	50 (17.3)	50 (14.4)	25 (7.1)	25	25	0
September 29 V11-13, R6, 101 cm	10	73.3 (11.6)	NA[e]	65 --	8.3	NA	NA

[a]Phenological stage determined from criteria set forth in Fehr et al. (1971).

[b]Total: releases = 3; Large field cage: releases = 2; Backgrouns: releases = 2

[c]Predator-induced = Total - Background; Ground = Large field cage - Background; Foliage = Predator-induced - Ground

[d]All negative values (by calculation) have been set equal to zero.

[e]No releases made within the large field cage.

Figure 11. Patterns of mean daily mortality for medium velvetbean caterpillar larvae at Green Acres, 1981.

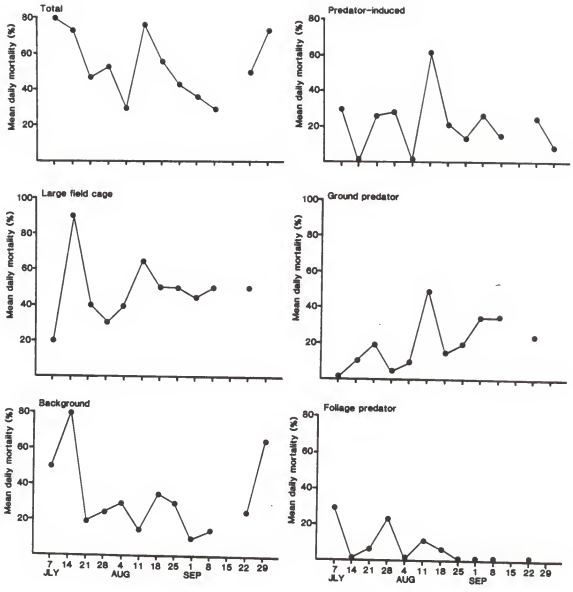

Total
Predator-induced
Large field cage
Ground predator
Background
Foliage predator
Mean daily mortality (%)
20
40
60
80
100
7 14 21 28 4 11 18 25 1 8 15 22 29
JLY
AUG
SEP

Table 18. The percent mean daily mortality estimates for large velvetbean caterpillar larvae at Green Acres, 1981.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
July 7 V2-3, 27 cm	5	100 ---	0 -	20 (28.3)	80	0	80
July 14 V3-4, 43 cm	5	93.3 (11.6)	100 ---	70 (14.1)	23.3	30	0[d]
July 21 V5-6, 63 cm	10	50 (17.3)	40 --	10 --	40	30	10
July 28 V7-8, R1-2, 70 cm	10	86.7 (11.6)	50 --	35 (21.2)	51.7	15	36.7
August 4 V11-12, R2, 77 cm	10	46.7 (15.3)	20 (14.1)	35 (5)	11.7	0[d]	11.7
August 11 V11-13, R2, 90 cm	5	93.3 (11.6)	40 --	60 --	33.3	0[d]	33.3
August 18 V11-13, R3-4, 90 cm	5	70 (17.3)	30 (14.1)	0 -	70	30	40
August 25 V11-13, R5, 93 cm	5	40 (69.3)	40 --	40 (56.6)	0	0	0
September 1 V11-13, R5-6, 98cm	7	47.6 (8.2)	50 (50.5)	21.4 (37.1)	26.2	28.6	0[d]

Table 18. continued.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
September 8 V11-13, R5-6, 100 cm	5	40 (20)	40 (28.3)	20 --	20	20	0
September 15 V11-13, R6, 101 cm	10	----------	----------	RAINED OUT	----------	----------	----------
September 22 V11-13, R6, 102 cm	9	55.6 (19.2)	61.1 (7.9)	33.3 ----	22.3	27.8	0[d]
September 29 V11-13, R6, 101 cm	5	66.7 (23.1)	NA[e]	20 (28.3)	46.7	NA	NA

[a]Phenological stage determined from criteria set forth by Fehr et al. (1971).

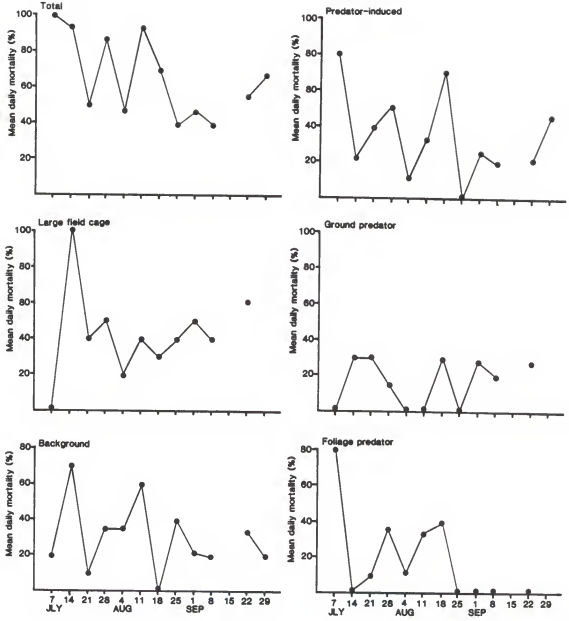
[b]Total: releases = 3; Large field cage: releases = 2; Background: releases = 2

[c]Predator-induced = Total - Background; Ground = Large field cage - Background; Foliage = Predator-induced - Ground

[d]All negative values (by calculation) have been set equal to zero.

[e]No releases were made within the large field cage.

Figure 12. Patterns of mean daily mortality for large velvetbean caterpillar larvae at Green Acres, 1981.


Total
Predator-induced
Large field cage
Ground predator
Background
Foliage predator
Mean daily mortality (%)
100
80
60
40
20
7 14 21 28 4 11 18 25 1 8 15 22 29
JLY
AUG
SEP

10-80% for medium larvae, and 10-70% for large larvae (Tables 15-18 and Figures 9-12).

The number of eggs hatching during a 24 hour period, determined from hatch of eggs held in a petri dish in the insectary, was zero on all dates except 21 July when it was 1 out of 25 (4%). Therefore, the assumption that missing eggs fell victim to some agent of mortality appeared reasonable.

Releases of eggs dusted with wing moth scales (dusted eggs) to determine the effects of laboratory preparation on the mortality inflicted on eggs, resulted in estimates of mean daily total mortality that ranged from 50-90% (Figure 9). Comparisons of the estimates of total mortality of dusted and non-dusted eggs revealed no significant differences (8 September: $t_{2df} = -1.15$, $P > 0.4$; 15 September: $t_{2df} = -1.31$, $P > 0.3$; 22 September: $t_{2df} = -0.13$, $P > 0.5$; 29 September: $t_{2df} = 0.50$, $P > 0.5$). These results suggest that the procedures used to collect eggs from moths in a laboratory culture did not affect the amount of mortality inflicted on eggs placed in the field. These results also suggest either an absence of a VBC kairomone, the lack of response by arthropod predators to such a chemical, or some combination thereof. More research is needed to establish the presence or absence of a VBC kairomone, and the response of arthropod predators.

Estimates of total, large field cage, and background mortality were compared for each life stage by means of a 2-way ANOVA procedure with time and type of mortality as factors. For each life stage, the mortality estimates varied significantly through time (Table 19) which indicated that the estimates of the 3 types of

Table 19. Comparisons of the estimates of total, large field cage, and background mortality of velvetbean caterpillar eggs and larvae in 1981. Time and type of mortality were used as factors.

Source	degrees of freedom	Sums of Squares	Mean Squares	F	P > F
		Eggs			
Week	11	5124.65	465.88	3.84	0.004
Mortality	2	4626.28	2313.14	19.08	0.001
Error	22	2666.53	121.21		
Total	35	12417.46			
		Small Larvae			
Week	10	8225.09	822.51	3.60	0.007
Mortality	2	1839.30	919.65	4.02	0.034
Error	20	4573.68	228.68		
Total	32	14638.08			
		Medium Larvae			
Week	10	6252.11	625.21	3.00	0.017
Mortality	2	2988.11	1494.06	7.18	0.005
Error	20	4164.01	208.20		
Total	32	13404.23			
		Large Larvae			
Week	10	8888.46	888.85	2.50	0.039
Mortality	2	6748.65	3374.32	9.50	0.001
Error	20	7104.77	355.24		
Total	32	22741.87			

mortality had to be compared on each date. These comaprisons were made using an 1-way ANOVA procedure. For most dates, there were no significant differences among the mortality estimates of each stage (Table 20). For those few dates on which at least 1 of the estimates differed, a Duncan's Multiple Range test was performed to determine differences among the estimates. The results of this analysis can be found in Table 20.

In 1982, the estimates of mean daily mortality of small larvae varied from 34-90% over the season (Table 21 and Figure 13). The estimates of large field cage mortality and background mortality ranges from 38-80% and 18-94%, respectively (Table 21 and Figure 13).

The estimates of total, large field cage, and background mortality of small larvae in 1982 were compared by means of a 2-way ANOVA procedure with time and type of mortality as factors. The mortality estimates did not vary significantly through time (Table 22). The estimates of the 3 types of mortality differed statistically (Table 22), and in general the estimates were ranked from largest to smallest in the following order: total, large field cage, and background (Table 21).

Estimates of mean daily total mortality of small VBC larvae in 1981 and 1982 showed some consistency with those determined by Luna (1979) who found that mean daily total mortality of small VBC larvae in soybeans ranged from 35.1-64.9% over 5 weeks in midseason. Comparisons of the 95% confidence limits revealed overlap of the limits on 3 out of 5 dates for estimates from 1981 and on 4 out of 5 dates for estimates from 1982 (Table 23). The

Table 20. Comparisons of the total, large field cage, and background mortality estimates for velvetbean caterpillar immatures at Green Acres, 1981.

Date	Egg	Small Larvae	Medium Larvae	Large Larvae
July 7	$F_{2,4df} = 3.6$	$F_{2,3df} = 4.9$	$F_{2,3df} = 1.7$	$F_{2,3df} = 21.6$[a]
July 14	$F_{2,4df} = 0.3$	$F_{2,4df} = 15.7$[b]	$F_{2,4df} = 0.8$	$F_{2,4df} = 4.4$
July 21	$F_{2,4df} = 0.4$	$F_{2,2df} = 0.4$	$F_{2,4df} = 1.38$	$F_{2,3df} = 4.9$
July 28	$F_{2,4df} = 3.0$	$F_{2,4df} = 2.2$	$F_{2,4df} = 4.5$	$F_{2,4df} = 2.5$
August 4	$F_{2,4df} = 8.9$[c]	$F_{2,4df} = 2.6$	$F_{2,4df} = 0.7$	$F_{2,4df} = 3.3$
August 11	$F_{2,4df} = 6.1$	$F_{2,4df} = 2.5$	$F_{2,4df} = 7.0$[d]	$F_{2,2df} = 9.2$
August 18	$F_{2,4df} = 1.0$	$F_{2,4df} = 6.6$	$F_{2,4df} = 0.9$	$F_{2,2df} = 18.5$[e]
August 25	$F_{2,4df} = 3.1$	$F_{2,4df} = 4.9$	$F_{2,4df} = 0.2$	$F_{2,2df} = 0$
September 1	$F_{2,4df} = 0.5$	$F_{2,4df} = 0.2$	$F_{2,4df} = 1.8$	$F_{2,4df} = 0.6$
September 8	$F_{2,4df} = 3.8$	$F_{2,4df} = 3.0$	$F_{2,4df} = 5.5$	$F_{2,4df} = 0.7$
September 15	$F_{2,4df} = 2.1$	Rain	Rain	Rain

Table 20. continued.

Date	Egg	Small Larvae	Medium Larvae	Large Larvae
September 22	$F_{2,4df} = 2.1$	$F_{2,4df} = 2.8$	$F_{2,4df} = 2.1$	$F_{2,4df} = 2.2$
September 29	$F_{1,3df} = 1.8$	$F_{1,3df} = 0.4$	$F_{1,3df} = 2.1$	$F_{1,3df} = 4.2$

[a] $P < 0.025$; 100a(Total) > 20b(Large field cage) > 0b(Background) [Means not followed by the same letter significant at the 0.05 level]

[b] $P < 0.025$; 100a(Total) > 70b(Background) > 50b(Large field cage) [Means not followed by the same letter significant at the 0.05 level]

[c] $P < 0.05$; 80a (Large field cage) > 76.7a(Total) > 40b(Background) [Means not followed by the smae letter significant at the 0.05 level]

[d] $P < 0.05$; 76.7a(Total) > 65ab(Large field cage) > 15b(Background) [Means not followed by the same letter significant at the 0.05 level]

[e] $P < 0.05$; 70a(Total) > 30b(Large field cage) > 0b(Background) [Means not followed by the same letter significant at the 0,05 level]

Table 21. The mean daily mortality estimates for small velvetbean caterpillar larvae at Green Acres, 1982.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
July 6 V4, 24 cm	7	85.7 (17.5)	48.6 (12.8)	37.1 (21.7)	48.6	11.4	37.1
July 13 V5-6, 30 cm	10	68 (13)	38 (11)	30 (14.1)	38	8	30
July 20 V6-8, 41 cm	7	48.6 (29.6)	42.9 (20.2)	31.4 (12)	17.1	11.4	5.7
July 27 V10-11, R1-2, 50 cm	6	77.8 (17.1)	72.3 (25.5)	50 --	27.8	22.2	5.6
August 3 V11-14, R2, 62 cm	10	34 (39.8)	44 (21.9)	18 (8.4)	16	26	0[d]
August 10 V12-13, R2, 69 cm	7	37.1 (27.9)	80 (21.7)	22.9 (16.7)	14.3	57.1	0[d]
August 17 V11-13, R3, 78 cm	9	53.3 (34.6)	48.9 (16.9)	40 (12.7)	13.3	8.9	4.5
August 24 V11-13, R4-5, 81 cm	9	71.1 (14.9)	55.6 (15.7)	46.7 (14.5)	24.4	8.9	15.6

Table 21. continued.

Date, Stage[a], and Height	Number Released	Total[b] Mean (SD)	Large Field Cage[b] Mean (SD)	Background[b] Mean (SD)	Predator-Induced[c]	Ground[c]	Foliage[c]
August 31 V11-13, R4-5, 78 cm	10	50 (12.5)	66 (20.7)	94[e] (8.9)	0[d]	0[d]	0[d]
September 7 V11-14, R5, 80 cm	10	64 (18.2)	66 (21.9)	52 (13)	12	14	0[d]
September 14 V11-14, R6, 80 cm	6	90 (14.9)	80 (13.9)	23.3 (22.4)	66.7	56.7	10

[a]Phenological stage determined from criteria set forth by Fehr et al. (1971).

[b]Total, Large field cage, and Background: releases = 5

[c]Predator-induced = Total - Background; Ground = Large field cage - Background; Foliage = Predator-induced - Ground

[d]Negative values (by calculation) have been set equal to zero.

[e]Problems with high mortality with the larvae released in the field cages.

Figure 13. Patterns of mean daily mortality for small velvetbean caterpillar larvae at Green Acres, 1982.

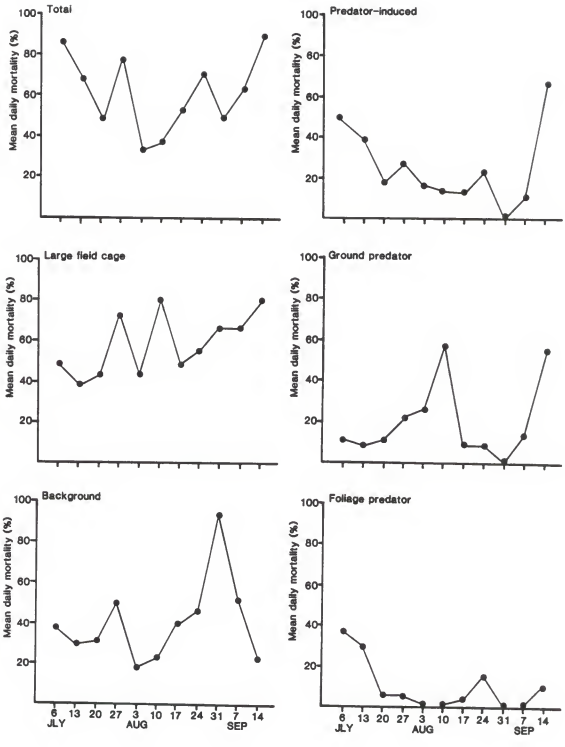

Total
Predator-induced
Large field cage
Ground predator
Background
Foliage predator
Mean daily mortality (%)
100
80
60
40
20
6 13 20 27 3 10 17 24 31 7 14
JLY
AUG
SEP

Table 22. Comparisons of the estimates of total, large field cage, and background mortality of small velvetbean caterpillar larvae in 1982. Time and type of mortality were used as factors.

Source	degrees of freedom	Sums of Squares	Mean Squares	F	P > F
Weeks	10	4255.50	425.55	1.42	0.10
Mortality	2	2877.31	1438.66	4.79	0.05
Error	20	6002.69	300.13		
Total	32	13135.50			

Table 23. The 95% confidence limits for the estimates of mean daily total mortality of small velvetbean caterpillar larvae from 1981 and 1982 compared with those from Luna (1979).

Date	Luna			1981			1982		
	Upper	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower
July 13 - 17	48.6	41.5	34.4	-	100	-	84.2	68	51.8
July 20 - 24	49.8	43.5	37.2	76.5	55	33.5	85.4	48.6	11.8
July 27 - 31	72.2	64.2	56.3	135.7	70	4.3	93.2	77.8	62.4
August 3 - 7	74.3	64.9	55.5	125.0	73.3	21.7	83.4	34	-15.4
August 10 - 14	44.6	35.1	25.6	111.0	96.7	82.3	71.7	37.1	2.6

lack of overlap on the remaining dates cannot be attributed to any particular factor or group of factors, due to a lack of information.

Comparisons of the estimates of mortality of small and medium VBC larvae among years were performed by means of a 2-way ANOVA procedure with weeks and years as factors. The estimates used in the comparisons were from weeks in which the plants were in similar phenological stages and had suffered similar amounts of defoliation. For small larvae, the estimates of total, large field cage, and background mortality estimates did not differ significantly from week to week or from year to year (Table 24). For medium larvae, only estimates of total mortality could be compared and these were found not to differ significantly from week to week or year to year (Table 24). This suggests that the estimates of mortality of small and medium larvae remained constant throughout the season and from year to year.

Estimates of daily total mortality can be partitioned into the mortality induced by all predators (predator-induced mortality) and that induced by factors other than predators (background mortality). The predator-induced mortaltiy can then be further partitioned according to the position in the habitat occupied by the predator (ground or foliage). To estimate these mortality components, the following formulae were used:

Predator-Induced Mortality = Total Mortality - Background Mortality

Ground Predator Mortality = Large Field Cage Mortality - Background Mortality

Foliage Predator Mortality = Predator-Induced Mortality - Ground Predator Mortality

Table 24. Comparisons of the estimates of total, large field cage, and background mortality of small velvetbean caterpillar larvae and of the estimates of total mortality of medium velvetbean caterpillar larvae among years.

Source	degrees of freedom	Sums of Squares	Mean Squares	F	P > F
		Small Larvae Total			
Weeks	9	3899.05	433.23	1.2	0.35
Year	2	1588.22	794.11	2.2	0.14
Error	18	6500.27	631.13		
Total	29	11987.54			
		Small Larvae Large Field Cage			
Weeks	9	1765.97	196.22	0.59	0.78
Year	1	480.81	480.81	1.44	0.26
Error	8	2665.45	333.18		
Total	18	4912.23			
		Small Larvae Background			
Weeks	9	4460.72	495.64	0.96	0.52
Year	1	100.68	100.68	0.20	0.67
Error	9	4634.98	514.99		
Total	19	9196.37			
		Medium Larvae Total			
Weeks	9	1987.53	220.84	1.15	0.42
Year	1	642.07	642.07	3.33	0.10
Error	9	1733.54	192.61		
Total	19	4363.14			

Any partitioned estimate of mortality whose value was less than zero as a result of application of the above formulae, was set equal to zero.

In 1981, the estimates of partitioned mortality of eggs and larvae varied over the season. The estimates of predator-induced mortality ranged from 1.7-45% for eggs, 0-53.3% for small larvae, 0-61.7% for medium larvae, and 11.7-89% for large larvae (Tables 15-18 and Figures 9-12). The estimates of mortality inflicted by ground predators had a range of 0-55% for eggs, 0-40% for small larvae, 0-50% for medium larvae, and 0-30% for large larvae (Tables 15-18 and Figures 9-12). The estimates of mortality inflicted by foliage predators ranged from 0-25% for eggs, 0-30% for small larvae, 0-30% for medium larvae, and 0-80% for large larvae (Tables 15-18 and Figures 9-12).

The estimates of the partitioned mortality for large larvae were greater than those for either of the other 2 types of larvae. This was due in part to the inability of the mark-release-recapture technique to distinguish between mortality and pupation. Both processes resulted in a loss of larvae from field and large field cage release sites. The proportion of larvae pupating during a release could not be determined because of the biotic and abiotic factors governing pupation were not well understood and none of the large larvae released within the small field cages pupated.

In 1982, the estimates of partitioned mortality for small VBC larvae ranged from 0-66.7% for predator-induced mortality, 0-51.1% for ground predator mortality, and 0-37.1% for foliage predator mortality (Table 21 and Figure 13).

For both 1981 and 1982, estimates of ground predator mortality were overestimates of the mortality inflicted by ground dwelling predators. The first of 2 reasons for this overestimation was that the large field cage used in estimating ground predator mortality reduced the competition for VBC immatures between ground and foliage predators. This allowed the ground predators to have greater access to the immatures. The second reason for the overestimation was that the actual ground predator mortality was a function of the frequency with which ground predators searched the foliage for prey, the frequency with which VBC immatures fell to the ground, and the frequency with which VBC immatures returned to the plant after falling. The last 2 frequencies take on a value of zero for the egg stage because eggs do not readily fall to the ground. To incorporate these frequencies and correct the ground predator mortality, the following formula can be used:

Corrected Ground Predator Mortality = (Ground Predator Mortality X Frequency of Foliage Search by Ground Predators) + (Ground Predator Mortality X Frequency of Fall) - (Ground Predator Mortality X Frequency of Return)

To correct the ground predator mortality using this relationship requires estimates of the 3 frequencies. In 1982, 2 of the 3 frequencies were estimated. The frequency of foliage search by ground predators was estimated indirectly from direct observation and was found to be equal to zero because few ground predators were observed on the foliage searching for prey. The frequency of fall was estimated directly each week and was found to remain relatively constant throughout the season increasing only with the incidence of rainstorms (Table 25). The frequency of return

Table 25. Estimates of the frequency of fall of small velvetbean caterpillar (VBC) larvae at Green Acres, 1982 and some factors that may influence it.

Date	Frequency of Fall	Ground Area per trap (cm^2)	Leaf Area per trap (cm^2)	Canopy Temperature	Predator per 91 cm of row	Small VBC larvae per 91 cm of row	Rain[a]
July 6	0.1174	1150	4350	26.6	0.6	0	0
July 13	0.1313	1391.5	5235	29.6	0.5	0	0
July 20	0.2333	1828.5	12975	27.6	0.8	0.2	+
July 27	0.24	1966.5	14842.5	24.8	4.4	0	+
August 3	0.1333	2334.5	22777.5	27.7	2.9	1.5	0
August 10	0.2236	2673.75	27142.5	27	5.2	3.6	+
August 17	0.1438	3001.5	30697.5	26.5	3.9	2.7	+
August 24	0.1471	2438	38197.5	27.1	4.6	8.1	0
August 31	0.14	2438	26947.5	26.4	2.7	10.2	0
September 7	0.11	3133.75	32542.75	25.2	2.7	14.1	0
September 14	0.15	3220	24735	27.6	3.95	2.1	0

[a] + = rain storm; 0 = no rain storm

of small larvae was assumed to be zero. By substituting these frequencies into the above relationship, the corrected ground predator mortality could be calculated for each week. In addition, the foliage predator mortality could be corrected for the overestimation of ground predator mortality by subtracting the corrected ground predator mortality from the predator-induced mortality. The corrected ground predator mortality and corrected foliage predator mortality estimates ranged from 0-12.8% and 0-57.6%, respectively (Table 26).

To eliminate the need for correcting ground predator mortality in future experiments, the predator-induced mortality should be partitioned according to the place in the habitat where the predation occurs regardless of the species of the predator inflicting mortality. This modification eliminates the need for classification of predators as ground or foliage predators. Such classification becomes difficult when predators, such as ants, forage on both the foliage and on the ground. By partitioning the predator-induced mortality according to the place in the habitat where the predation occurs, the estimates of mortality due to ground predation would be replaced by estimates of the mortality due to predation events on the ground which can be estimated from the frequency of fall of VBC immatures, the probability that VBC immatures are consumed by a predator once on the ground, and the densities of VBC immatures and predators that are active on the ground.

In summary, the mean dialy rates of total, large field cage, and background mortality for small larvae, and the mean daily rates of total mortality for medium larvae remained constant from year

Table. 26. The mean daily partitioned mortality estimates for small velvetbean caterpillar larvae at Green Acres, 1982, corrected by inclusion of the estimates of frequency of fall.

Date	Predator-Induced	Ground	Frequency of Fall	Corrected Ground[a]	Corrected Foliage[a]
July 6	48.6	11.4	0.1174	1.3	47.3
July 13	38	8	0.1313	1.1	36.9
July 20	17.1	11.4	0.2333	2.7	14.4
July 27	27.8	22.2	0.24	5.3	22.5
August 3	16	26	0.1333	3.5	12.5
August 10	14.3	57.1	0.2236	12.8	1.5
August 17	13.3	8.9	0.1438	1.3	12
August 24	24.4	8.9	0.1471	1.3	23.1
August 31[b]	0	0	0.14	0	0
September 7	12	14	0.11	1.5	10.5
September 14	66.7	56.7	0.15	8.5	58.2

[a]Corrected Ground = Ground*Frequency of Fall; Corrected Foliage = Predator-Induced - Corrected Ground

[b]Problems with larvae released in the background releases.

to year. The seasonal mean daily rates of predation mortality were about 24% for eggs, 25% for small larvae, 23% for medium larvae, and 35% for large larvae given prey densities ranging from 5-10 individuals per 91 cm of row. The predation mortality for large larvae was confounded with the loss of larvae due to pupation. The estimates of mean daily ground predator mortality for all stages were overestimates of the actual ground predator mortality. These estimates could be corrected if the frequency of foliage search by ground predator and the frequency of fall were known.

Partitioning of Predator-Induced Mortality by Species

In 1981 and 1982, the number of predation events recorded was not sufficient to allow the partitioning of the predator-induced mortality according to predator species. Instead, the results from direct observation were used to identify those predator species that could be considered as the major contributors to predation mortality.

In 1981, the direct observation technique used for observing foliage predation events seemed to work well for small and medium larvae, but was poor for observing predation on eggs and large larvae. Of the 35 total foliage prey records, 30 were of predators preying upon small and medium larvae (Table 27). The large number of records for these 2 stages was probably due in part to the amount of time necessary for a predator to capture and consume a prey item. The predators of eggs and large larvae can either quickly consume, or capture and carry the prey to another location to consume it. Some of the predators of small and medium larvae, on the other hand, remain at the site of capture for considerable

Table 27. Summary of the observations of foliage predation events on velvetbean caterpillar eggs and larvae at Green Acres, 1981. (Total = 46)

Predator species	Proportion consumed
Eggs (total = 4)	
Unknown: damaged eggs	0.50
Spanogonicus albofasciatus (Reuter) adult	0.25
Geocoris punctipes (Say) nymph	0.25
Small Larvae (total = 11)	
Tropiconabis capsiformis (Germar) adult	0.28
Oxyopes salticus Hentz	0.18
Clubionidae immature	0.18
Tropiconabis capsiformis (Germar) nymph	0.09
Geocoris punctipes (Say) nymph	0.09
Misumenops spp.	0.09
Nabis roseipennis Reuter nymph	0.09
Medium Larvae (total = 19)	
Tettigoniidae	0.26
Podisus maculiventris (Say) nymph	0.11
Calleida decora (F.) larvae	0.11
Chiracanthium inclusum (Hentz)	0.11
Misumenops spp.	0.11
Geocoris punctipes (Say) adult	0.05
Tropiconabis capsiformis (Germar) nymph	0.05
Zelus spp. adult	0.05
Labidura riparia (Pallas) nymph	0.05
Clubionidae	0.05
Hentzia palmarum (Hentz)	0.05

Table 27. continued.

Predator species	Proportion consumed
Large Larvae (total = 1)	
Tettigoniidae	1.0

time to consume a prey item. This increases the probability of being observed.

The small number of observation records for large larvae may also be due to the limited number of predator species capable of capturing a large larva because of its size and violent behavior when disturbed. Small and medium larvae also demonstrate this defensive behavior, but because of their smaller size, they can be more easily captured by many of the foliage predators. Therefore, the number of predator species capable of capturing a large larva is smaller than those capable of capturing an egg, or a small or medium larva.

The total number of foliage predation events for eggs was 4 with the greatest proportion of mortality attributable to unknown causes (Table 27). Two predators, Spanogonicus albofasciatus (Reuter) and Geocoris punctipes, were observed preying upon eggs (Table 27).

Eggs dusted with VBC moth scales were placed with non-dusted eggs at egg stations on 15 and 22 September to determine if the non-dusted eggs were less attractive than those dusted with moth scales. If dusted eggs were more attractive to predators, then the ratio of dusted eggs missing in a 24 hour observation period to non-dusted eggs missing in the same 24 hour period should be greater than the ratio of dusted eggs to non-dusted eggs maintained at egg stations throughout the field. The 2 ratios did not differ statistically on either date (15 September: $\chi^2_{1df} = 3.34$, $0.10 > P > 0.05$; 22 September: $\chi^2_{1df} = 3.76$, $0.10 > P > 0.05$). This suggests that the predators were not selecting dusted eggs over non-dusted eggs.

The total number of foliage observations for small larvae was 11 with Tropiconabis capsiformis adults consuming the greatest proportion (Table 27). This predator was also the major predator of small larvae at Green Acres in the 1980 field season (Table 8). In 1980, more spiders were observed feeding on small larvae than in 1981 (Tables 8 and 27). High ambient and soil temperatures experienced in 1981 also inflicted some mortality that was not observed in the 1980 field season.

Tettigoniids were observed to consume 5 out of the 19 total medium larvae that were observed being preyed upon (Table 27). Podisus maculiventris (Say), Calleida decora (F.), and Chiracanthium inclusum (Hentz) were observed to consume the next greatest proportion of medium larvae (Table 27). The predators observed consuming medium larvae were approximately the same in 1980 and 1981 (Tables 8 and 27). The major difference between the years was a shift from Nabis roseipennis to tettigoniids as the major consumer of medium larvae.

The total number of foliage predation observations for large larvae was 1. A tettigoniid was the only predator seen consuming a large larva (Table 27). Various Hymenoptera were seen near observation stations with large larvae, but no observations were made of wasps taking larvae.

The effect of the density of prey placed at a station on the number of predation events observed could not be examined. On the 2 dates on which 1 observation circle was run at maximum density, and the other, at minimum density, no predation events were recorded.

The total number of observations of predation on the ground for all stages of larvae was 407 (Table 28). As expected, more small larvae were attacked than medium larvae or large larvae, and small larvae had the lowest probability of escape from attack. Large larvae had the best ability to survive attacks by ground predators because of their size and defensive behavior (Table 28).

For small larvae, a total of 220 successful attacks and 27 unsuccessful attacks was observed. The ant, Pheidole morrisi Forel, was observed to consume the greatest proportion of small larvae (Table 28). The proportion of small larvae surviving attack was 0.11 (Table 28).

A total of 138 successful attacks and 86 unsuccessful attacks was observed on medium larvae. P. morrisi was observed to capture the greatest proportion of medium larvae (Table 28). On several occasions, it was observed that an individual ant would make contact with a medium or large larva and then would leave a station. A short while later, a large number of ants would swarm the area and capture all the larvae present at a station. The swarm of Pheidole ants was usually large enough to capture 4-5 medium larvae in one 10 minute period. The proportion of medium larvae surviving attack was 0.38 (Table 28).

For large larvae, a total of 49 successful attacks and 98 unsuccessful attacks was recorded. The ant, P. morrisi, had the greatest proportion of successful attacks (Table 28). The scouting and swarming behavior of Pheidole ants, described above, was also seen to occur with large larvae. The proportion of large larvae surviving attack was 0.67 (Table 28).

Table 28. Summary of observations of ground predation events of velvetbean caterpillar larvae at Green Acres, 1981. (Total = 407)

Predator species	Proportion attacked
Small Larvae	
Successful attacks (total = 220)	
Pheidole morrisi Forel	0.47
Pheidole dentata Mayr	0.20
Labidura riparia (Pallas) nymph	0.16
Solenopsis geminata (F.)	0.09
Labidura riparia (Pallas) adult	0.06
Conomymra spp. (black form)	0.01
Pardosa milvina (Hentz)	0.01
Unsuccessful attacks (total = 27)	
Pheidole dentata Mayr	0.41
Pheidole morrisi Forel	0.37
Labidura riparia (Pallas) nymph	0.11
Solenopsis geminata (F.)	0.07
Pardosa milvina (Hentz)	0.04
Medium Larvae	
Successful attacks (total = 138)	
Pheidole morrisi Forel	0.40
Pheidole dentata Mayr	0.17
Labidura riparia (Pallas) adult	0.14
Solenopsis geminata (F.)	0.14
Labidura riparia (Pallas) nymph	0.12
Doru lineare (Escholtz) nymph	0.01
Pardosa milvina (Hentz)	0.01

Table 28. continued.

Predator species	Proportion attacked
Medium Larvae	
Unsuccessful attacks (total = 86)	
Pheidole morrisi Forel	0.41
Pheidole dentata Mayr	0.30
Labidura riparia (Pallas) nymph	0.23
Labidura riparia (Pallas) adult	0.03
Solenopsis geminata (F.)	0.01
Pardosa milvina (Hentz)	0.01
Large Larvae	
Successful attacks (total = 49)	
Pheidole morrisi Forel	0.31
Pheidole dentata Mayr	0.27
Solenopsis geminata (F.)	0.18
Labidura riparia (Pallas) adult	0.16
Labidura riparia (Pallas) nymph	0.08
Unsuccessful attacks (total = 98)	
Pheidole morrisi Forel	0.44
Pheidole dentata Mayr	0.24
Labidura riparia (Pallas) nymph	0.18
Labidura riparia (Pallas) adult	0.07
Solenopsis geminata (F.)	0.03
Pardosa milvina (Hentz)	0.02
Conomyrma spp. (black form)	0.01

High temperatures, both canopy and soil surface temperatures (summarized in Appendix A), were responsible for some of the observed mortality. At the foliage stations, 3 small, 3 medium, and 5 large larvae succumbed to the high canopy temperatures. The larvae that died from heat appeared to be desiccated. At the ground stations, 4 small, 3 medium, and 6 large larvae died from the heat. An effort was made to place larvae in shaded areas to minimize the mortality due to high temperatures.

Most of the observations were recorded between 10 am and 9 pm for the foliage predation events (Table 29), 5 am-6 pm for the successful ground predation events, and 8 am-6 pm for the unsuccessful attempts of ground predation (Table 30). The large amount of predation activity occurring in these time periods may have been due in part to the specific time of day each species of arthropod predators were foraging. The most notable for foraging periodicity were clubionid spiders, Misumenops spp., and Oxyopes salticus Hentz on the foliage (Table 29), and Labidura riparia (Pallas), P. morrisi, P. dentata Mayr, and Solenopsis geminata (F.) on the ground (Table 30).

Temperature may also have played a role in determining the time of day when predators were most active (temperatures summarized in Appendix A). Most observations of foliage predation events were recorded when mean canopy temperatures ranged from 22-31°C (Table 31). Most of the observations of ground predation events were recorded when the soil temperatures ranged 24-29°C for both successful and unsuccessful ground predation events (Table 32).

Table 29. The percent of predation events observed at each time of day on the foliage at Green Acres, 1981.

Predator species	Time of Day				
	8:00am-noon	12:01pm - 4:00pm	4:01pm-9:00pm	midnight-2:00am	5:00am-7:30am
Total	21.2	33.3	24.2	6.1	15.2
Tropiconabis capsiformis (Germar)	3.0	9.1	3.0	0	0
Geocoris punctipes (Say)	0	6.1	3.0	0	0
Labidura riparia (Pallas)	0	0	3.0	0	0
Zelus spp.	0	3.0	0	0	0
Clubionidae	0	0	0	3.0	12.1
Tettigoniidae	6.1	3.0	9.1	0	0
Misumenops spp.	6.1	3.0	0	0	0
Oxyopes salticus Hentz	0	0	3.0	3.0	0
Spanogonicus albofasciatus (Reuter)	3.0	0	0	0	0
Hentzia palmarum (Hentz)	0	0	3.0	0	0
Podisus maculiventris (Say)	3.0	3.0	0	0	0
Calleida decora (F.)	0	6.1	0	0	0
Nabis roseipennis Reuter	0	0	0	0	3.0

Table 30. The percent of predation events observed at each time of day on the ground at Green Acres, 1981.

Predator species	Time of Day 8:00am–noon	12:01pm–4:00pm	4:01pm–9:00pm	midnight–2:00am	5:00am–7:30am
			SUCCESSFUL		
Total	33.8	35.0	17.0	3.2	11
Labidura riparia (Pallas)	6.8	2.9	1.9	2.2	8.8
Pheidole morrisi Forel	19.7	12.4	4.9	0.5	1.7
Pheidole dentata Mayr	6.3	8.3	4.6	0.2	0.5
Conomymra spp. (black form)	0.2	0.2	0	0	0
Doru lineare (Escholtz)	0.5	0	0	0	0
Pardosa milvina (Hentz)	0	0.5	0	0	0
Solenopsis geminata (F.)	0.2	6.6	4.6	0.2	0
			UNSUCCESSFUL		
Total	31.7	32.2	18.3	9.1	8.7
Labidura riparia (Pallas)	7.2	2.9	2.4	4.8	5.3
Pheidole morrisi Forel	13.5	18.3	6.3	2.9	2.9
Pheidole dentata Mayr	10.1	8.7	7.2	1.4	0.5
Pardosa milvina (Hentz)	0	1.9	0	0	0
Solenopsis geminata (F.)	1.0	0.5	1.4	0	0

Table 31. The percent of predation events observed at each temperature range on the foliage at Green Acres, 1981.

Predator species	Temperature (°C)				
	16 - 19	22 - 26	28 - 31	33 - 35	37 - 41
Total	9.4	25	34.4	18.8	12.5
Tropiconabis capsiformis (Germar)	0	3.1	6.3	3.1	3.1
Geocoris punctipes (Say)	0	0	0	6.3	3.1
Labidura riparia (Pallas)	0	0	0	3.1	0
Zelus spp.	0	0	3.1	0	0
Clubionidae	6.3	9.4	6.3	0	0
Tettigoniidae	0	6.3	6.3	6.3	0
Oxyopes salticus Hentz	0	6.3	0	0	0
Spanogonicus albofasciatus (Reuter)	0	0	3.1	0	0
Podisus maculiventris (Say)	0	0	3.1	0	3.1
Calleida decora (F.)	0	0	3.1	0	3.1
Nabis roseipennis Reuter	3.1	0	0	0	0

Table 32. The percent of predation events observed at each temperature range on the ground at Green Acres, 1981.

Predator species	Temperature (°C) 19 - 23	24 - 26	27 - 29	30 - 32	33 - 35
			SUCCESSFUL		
Total	13.4	27.6	29.6	9.3	9.1
Labidura riparia (Pallas)	10.9	8.8	5.8	1.1	0
Pheidole morrisi Forel	2.5	12.9	19.7	5.2	1.4
Pheidole dentata Mayr	0	2.2	5.0	2.2	7.5
Conomyrma spp. (black form)	0	0	0	0.3	0
Doru lineare (Escholtz)	0	0	0	0	0.3
Pardosa milvina (Hentz)	0	0	0.3	0.3	0
Solenopsis geminata (F.)	0	3.8	8.0	0.3	0
			UNSUCCESSFUL		
Total	13.1	28.7	34.3	17.1	6.6
Labidura riparia (Pallas)	7.5	9.1	6.6	2.0	0.5
Pheidole morrisi Forel	2.0	13.1	14.7	18.1	3.0
Pheidole dentata Mayr	2.5	6.1	12.1	5.1	3.0
Pardosa milvina (Hentz)	0	0	1.0	0.5	0
Solenopsis geminata (F.)	1.0	0.5	0	1.5	0

For most of the foliage predators, the upper limit of their temperature range was exceeded from about noon until about 6 pm. The predation events recorded in this time were due to the actions of a few predator species that were active at slightly higher temperatures (Table 31). For the ground predators, the soil temperatures after canopy closure usually fluctuated between 24° and 29°C during the day, but dropped below 24°C from about midnight until about 6 am.

In 1982, a total of 32 foliage predation events on small VBC larvae was recorded. Geocoris punctipes adults and Calleida decora larvae were observed to consume the greatest proportion of larvae (Table 33). The predator species observed feeding upon small larvae in 1982 differed slightly from those observed in 1980 and 1981 (Tables 8, 27, and 33). The most notable difference was the drop in ranking of Tropiconabis capsiformis, the major consumer of small larvae at the direct observation stations in 1980 and 1981.

At the ground observation stations in 1982, a total of 84 successful and 38 unsuccessful predation events was observed (Table 34). Labidura riparia nymphs were observed to consume the greatest proportion of small larvae (Table 34). The proportion of small larvae surviving attack was 0.31 (Table 34). The ground predator species observed to consume small larvae in 1982 were very similar to those found in 1981 (Tables 28 and 34). The major difference between years was a shift in the major predator species from P. morrisi in 1981 to L. riparia in 1982.

Table 33. Summary of the observations of foliage predation events on small velvetbean caterpillar larvae at Green Acres, 1982. (Total = 32)

Predator species	Proportion consumed
Geocoris punctipes (Say) adults	0.16
Calleida decora (F.) larvae	0.16
Pheidole dentata Mayr	0.13
Tropiconabis capsiformis (Germar) adults	0.13
Metaphidippus galathea (Walckenear)	0.06
Salticidae immature	0.06
Tettigoniidae	0.06
Hoplistoscelis deceptivus (Harris) adult	0.06
Oxyopes salticus Hentz	0.03
Zelus spp. adult	0.03
Podisus maculiventris (Say) nymph	0.03
Nabis roseipennis Reuter adult	0.03
Nabis roseipennis Reuter nymph	0.03
Tropiconabis capsiformis (Germar) nymph	0.03

Table 34. Summary of the observations of ground predation events on small velvetbean caterpillar larvae at Green Acres, 1982. (Total = 122)

Predator species	Proportion attacked
Successful attacks (total = 84)	
Labidura riparia (Pallas) nymph	0.30
Conomyrma spp. (black form)	0.29
Labidura riparia (Pallas) adult	0.18
Pheidole dentata Mayr	0.12
Pheidole morrisi Forel	0.10
Pardosa milvina (Hentz)	0.02
Unsuccessful attacks (total = 38)	
Conomyrma spp. (black form)	0.32
Pheidole morrisi Forel	0.29
Labidura riparia (Pallas) nymph	0.24
Pheidole dentata Mayr	0.08
Pardosa milvina (Hentz)	0.08

Most of the observation records in 1982 were recorded between 10 am-8 pm for the foliage predation events (Table 35) and 6 am-10 am and noon-8 pm for both successful and unsuccessful ground predation events (Table 36). The peak times of observations may have been due in part to the behavior of the predator species responsible for the mortality because some species appeared to demonstrate foraging periodicity (Tables 35-36). Temperature may also have played a role in determining the peak times of observation. Most observation events were recorded between mean canopy temperatures between 25-33°C for foliage predation events (Table 37) and at soil temperatures between 23-29°C for ground predation events (Table 38). On most dates, the mean canopy temperature did not reach 25°C until after 9 am, and rarely did it exceed 33°C. The soil temperature was within the 23-29°C range for most of the summer (temperatures summarized in Appendix A).

In summary, the direct observation technique appeared to work well for observing foliage predation events on small and medium larvae and ground predation events for all size classes of larvae. Some modification of the technique will be required for observing predation events on eggs and large larvae. The key predator species identified using direct observation were similar over all years. The amounts of mortality attributable to each species, however, changed from year to year. The changes may have been due in part to environmental factors, such as temperature, which influences the behavior of the predator species.

Table 35. The percent of predation events observed on the foliage by each predator species on small velvetbean caterpillar larvae at Green Acres, 1982.

Predator species	Time of Day			
	6:00am-10:00am	10:01am-2:00pm	2:01pm-6:00pm	6:01pm-8:00pm
Total	6.5	41.9	35.5	16.1
Geocoris punctipes (Say)	0	3.2	9.7	3.2
Calleida decora (F.)	0	6.5	6.5	3.2
Pheidole dentata Mayr	3.2	0	6.5	0
Tropiconabis capsiformis (Germar)	0	9.7	3.2	3.2
Metaphidippus galathea (Walckenear)	0	6.5	0	0
Salticidae	0	3.2	3.2	0
Hoplistoscelis deceptivus (Harris)	0	3.2	0	3.2
Zelus spp.	0	0	3.2	0
Podisus maculiventris (Say)	0	3.2	0	0
Oxyopes salticus Hentz	0	0	3.2	0
Nabis roseipennis Reuter	3.2	3.2	0	0
Tettigoniidae	0	3.2	0	3.2

Table 36. The percent of predation events observed on the ground at each time of day on small velvetbean caterpillar larvae at Green Acres, 1982.

Predator species	Time of Day 6:00am–10:00am	10:01am–2:00pm	2:01pm–6:00pm	6:01pm–8:00pm
		SUCCESSFUL		
Total	34.1	17.9	27.3	10.7
Labidura riparia (Pallas)	20.1	4.8	7	3.6
Conomyrma spp. (black form)	3.6	9.5	11.9	2.4
Pheidole dentata Mayr	3.6	2.4	3.6	1.2
Pheidole morrisi Forel	4.8	0	3.6	2.4
Pardosa milvina (Hentz)	0	1.2	1.2	0
		UNSUCCESSFUL		
Total	31.6	42.1	21.1	5.3
Labidura riparia (Pallas)	10.5	5.3	5.3	0
Conomyrma spp. (black form)				
Pheidole dentata Mayr	5.3	0	0	2.6
Pheidole morrisi Forel	5.8	2.6	10.5	0
Pardosa milvina (Hentz)	0	7.9	0	0

Table 37. The percent of predation events observed on the foliage at each temperature interval on small velvetbean caterpillar larvae at Green Acres, 1982.

Predator species	Temperature (°C)			
	23 - 26	27 - 29	30 - 32	33 - 34
Total	29	22.8	35.5	12.9
Geocoris punctipes (Say)	3.2	3.2	9.7	0
Calleida decora (F.)	0	3.2	6.5	6.5
Pheidole dentata Mayr	12.9	0	0	0
Tropiconabis capsiformis (Germar)	3.2	3.2	6.4	0
Metaphidippus galathea (Walckenear)	0	0	6.4	0
Salticidae	0	3.2	3.2	0
Hoplistoscelis deceptivus (Harris)	3.2	3.2	0	0
Zelus spp.	0	0	0	3.2
Podisus maculiventris (Say)	3.2	0	0	0
Oxyopes salticus Hentz	0	0	0	3.2
Tettigoniidae	0	0	6.4	0

Table 38. The percent of predation events observed on the ground at each temperature on small velvetbean caterpillar larvae at Green Acres, 1982.

Predator species	Temperature (°C)			
	20 - 22	23 - 25	26 - 29	30 - 33
		SUCCESSFUL		
Total	11.9	21.1	45.2	10.7
Labidura riparia (Pallas)	8.3	27.4	9.5	2.4
Conomyrma spp. (black form)	0	0	21.4	7.1
Pheidole dentata Mayr	1.2	2.4	8.3	0
Pheidole morrisi Forel	2.4	2.4	3.6	1.2
Pardosa milvina (Hentz)	0	0	2.4	0
		UNSUCCESSFUL		
Total	13.2	31.6	44.7	10.4
Labidura riparia (Pallas)	0	15.8	7.9	0
Conomyrma spp. (black form)	0	0	31.3	5.3
Pheidole dentata Mayr	5.3	0	2.6	0
Pheidole morrisi Forel	7.9	7.9	7.9	5.3
Pardosa milvina (Hentz)	0	7.9	0	0

Estimates of Predator Population Densities

In 1981 and 1982, the species composition of the predator complexes appear similar, but there were fewer individuals in each species in 1982 than in 1981 (densities of foliage and ground predators are summarized in Appendix B). The mean relative densities of foliage dwelling species for both years increased as the season progressed, reaching peak population densities at the beginning of podfill stage. A similar increase was also noted in the relative densities and activities of ground dwelling predators as measured by pitfall traps in 1981. These increases in predator population densities on both the foliage and ground are consistent with the results of numerous other studies (Hasse 1971, Shepard et al. 1974a, Price and Shepard 1977, 1978, Marston et al. 1979, Bechinski and Pedigo 1981a). The influence of the time of day on the density of foliage dwelling predators appeared negligible in both 1981 and 1982.

In conclusion, the proposed method for quantifying arthropod predation provided estimates of the rates of mortality inflicted upon VBC eggs and larvae by all predators and by foliage and ground predators. The estimates of mortality inflicted by ground predators on all stages were inflated due to a lack of competition. These estimates can be corrected with estimates of the frequency of fall of each stage, the frequency of return to the plant after falling, and the frequency with which ground predators search the foliage for prey. The predator species responsible for the predation mortality were identified for small and medium larvae. However, some modification of the direct observation technique will be

required to identify the predator species responsible for the mortality on eggs and large larvae.

Notes

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THE IMPACT OF ARTHROPOD PREDATORS ON THE POPULATION DYNAMICS OF VELVETBEAN CATERPILLAR LARVAE

The method for quantifying arthropod predation on VBC eggs and larvae has generated a large body of data that can be used to estimate the parameter values for the initial multipredator model for VBC. To incorporate this information effectively into the model requires a quantitative description of the role of arthropod predators in VBC dynamics. Such description is based upon the examination of patterns of predator-induced mortality, and the response of a predator complex to changes in the universe searched.

In the studies presented, the information exists to allow examination of the seasonal patterns of mortality and the response of the predator complex to changes in the universe searched for small and medium larvae only. From this examination, the structure of the model required to represent the impact of arthropod predators on the dynamics of small and medium VBC larval populations can be determined and the parameter values estimated. To obtain sufficient information to determine the structure of the predation model for eggs and large larvae will require more intensive study of predation on these 2 stages. In the meantime, the model structure required to represent the impact of arthropod predators on eggs

and large larvae can be assumed to be similar to that for small and medium larvae. The values of the parameters of the model structure for these 2 stages can be estimated from the rates of predation determined in this study.

Visual examination of the patterns of predator-induced mortality for small and medium larvae revealed trends in the patterns of mortality for each stage over all years (Figures 3, 4, 10, and 11). For the small larvae, the pattern of predator-induced mortality was most notable in the estimates obtained in 1981 and 1982. The pattern was one in which the highest rates of predation were demonstrated early in the season. This was followed by a gradual decrease in the predation rates to a lower, rather constant level late in the season. For the medium larvae, the pattern of predator-induced mortality was one in which the rates of mortality remained relatively constant from 7 July through 1 September in 1980 and throughout the season in 1981. The pattern of predator-induced mortality after 1 September in 1980 was confounded with the effects of resource depletion. These observed patterns of predator-induced mortality may have been generated by an interaction of several processes that include the attraction of arthropod predators into a release site, expansion of the universe searched by a predator (i.e., the leaf area of the plant), and the response of the predator complex to prey and predator densities.

The attraction of arthropod predators into a release site may have aided in the generation of the patterns of predator-induced mortality by increasing the density of arthropod predators at a site, thereby increasing the probability of predation mortality.

Such increases in predator density in areas of high prey density are common in interactions of arthropod predators and aphid populations (Frazer et al. 1981, Ives 1981a). In this study, the attractiveness of the release sites was due to the artificially large densities of VBC larvae placed at a site, as required for mortality estimation. For much of the season, the release densities were greater than the densities of indigenous VBC larvae (Tables 5, 16, and 17; see Appendix B for densities of indigenous VBC larvae). For small larvae, the patterns of predator-induced mortality appear to reflect a decrease in attractiveness of larvae at a release site as the season progressed and the densities of indigenous, small VBC larvae increased. For the medium larvae, the pattern of predator-induced mortality appeared to reflect a continual attraction of predators to a release site throughout the season. This may be due to the release densities of medium larvae being comparable to field densities only on 1 or 2 sampling dates that occurred late in the season.

Confounded with the effect of attraction of arthropod predators into a release site is the increase in leaf area that predators must search to find prey. In soybeans, as in many row crops, the increase in leaf area from week to week during vegetative growth is tremendous (Shibles et al. 1975). Such increases in leaf area may effectively reduce the density of both predator and prey populations because recruitment into these populations may not be occurring at the same rate as the increase in leaf area. Reductions in the effective densities of predator and prey populations serve to reduce the probability of predator-prey encounters. This

can result in an apparent decrease in the mortality inflicted by arthropod predators in prey populations (Gutierrez et al. 1979).

To examine the effects of an increase in leaf area on predation mortality requires an examination of the response of the predator complex to prey and predator population densities. This is due to the dependency of the predator response on the physical characteristics of the universe searched by the predator (Huffaker and Kennett 1956, Huffaker et al. 1963, Murdoch and Oaten 1975). Examination of the response of the predator complex is facilitated by an initial investigation of the component responses, the response to prey density and the response to predator density, followed by an investigation of their combined effect.

To investigate the response of the predator complex to prey density, the relationship between the number of prey consumed per predator and changes in the prey density was determined. This response, although similar to Holling's (1959b) functional response, cannot be treated as such because the searching area, the availability of alternate prey, and the predator density were not held constant. To calculate the number of prey consumed per predator, the number of larvae released per unit leaf area (cm^2) was multiplied by the percent predator-induced mortality, and then this quantity was divided by the mean total predators per unit leaf area (cm^2). The leaf area estimates for 1980 were obtained from an independent study conducted in the same field by J. L. Stimac.[1] In 1981, the leaf area was not estimated; instead it was assumed to be the same as that estimated in 1982 by R. J. O'Neil[2] for plants in comparable phenological stages (see Appendix C for a summary of

leaf area). Simple linear regressions of the number of prey consumed per predator on prey density were performed for each stage and year to determine the response of the predator complex to prey density.

The results of this regression analysis showed a significant, positive relationship between the number of prey consumed per predator and prey density for the predator complexes preying upon small larvae in 1980 and 1982 (Tables 39-41). This response was similar to that found by Collins (1980) for a predator complex composed of Peucetia viridans (Hentz), Podisus maculiventris, Tropiconabis capsiformis, Labidura riparia, Hentzia palmarum (Hentz), Oxyopes salticus, and Calleida decora feeding upon VBC and soybean looper larvae within field cages.

The inconsistency in the response of the predator complex to prey density among years may be explained by 2 hypotheses. The first is that differences in the densities of prey species other than VBC (i.e., alternate prey) among years may have influenced the mortality inflicted by the predator complex on VBC larvae. The response of the predator complex to VBC densities, therefore, may be confounded with the effects of predator switching behavior and/or prey preference.

To examine this hypothesis, the ratio of the number of alternate lepidopterous prey to the number of VBC released was compared among years (see Appendix B for density estimates and comparisons). The ratio for weeks in which plants were in comparable phenological stages were compared. For small and medium lepidopterous prey, the ratios of alternate prey to VBC did not differ statistically

Table 39. The response of the predator complex to changes in the densities of small and medium velvetbean caterpillar larvae released at Green Acres and the response of the predator complex to changes in predator density. The values are ranked in order of increasing prey density.

Prey density (per cm^2)[a]	Predator density (per cm^2)[a]	Predator-induced mortality (%)	No. of prey consumed per predator
	Small Larvae		
0.0005	0.00025	10.84	0.216
0.0005	0.00016	0	0
0.0005	0.00036	25	0.347
0.0006	0.00023	12.5	0.326
0.0009	0.00072	6.67	0.084
0.0012	0.00019	20	1.26
0.0017	0.00017	10	1.0
0.0023	0.00018	0	0
0.0047	0.00042	20	2.2
$y = 417.27x + 0.006$, $F_{1,7df} = 10.3$, $(P > F) = 0.02$[b]			
$m = 0.95p + 8.90$, $F_{1,7df} = 0.29$, $(P > F) = 0.61$[c]			
	Medium Larvae		
0.0005	0.00025	0	0
0.0005	0.00016	10	0.47
0.0005	0.00036	0	0
0.0006	0.00023	27.5	0.724
0.0009	0.00072	0	0
0.0012	0.00019	32.5	1.91
0.0017	0.00017	37.5	3.75

Table 39. continued.

Prey density (per cm^2)[a]	Predator density (per cm^2)[a]	Predator-induced mortality (%)	No. of prey consumed per predator
	Medium Larvae		
0.0023	0.00018	5	0.625
0.0047	0.00042	10	1.11
$y = 243.06x + 0.61$, $F_{1,7df} = 0.57$, $(P > F) = 0.47$[b]			
$m = -3.88p + 24.97$, $F_{1,7df} = 2.10$, $(P > F) = 0.19$[c]			

[a] Leaf area estimates can be found in Appendix C.

[b] y = number of prey consumed per predator; x = prey density

[c] m = predator-induced mortality; p = predator density

Table 40. The response of the predator complex to changes in the densities of small and medium velvetbean caterpillar larvae released at Green Acres in 1981 and the response of the complex to changes in predator density. The values are ranked in order of increasing prey density.

Prey density (per cm^2)[a]	Predator density (per cm^2)[a]	Predator-induced mortality (%)	No. of prey consumed per predator
	Small Larvae		
0.0001	0.00008	3.33	0.056
0.0002	0.00017	3.33	0.036
0.0002	0.00012	0	0
0.0002	0.00010	10	0.172
0.0002	0.00014	0	0
0.0002	0.00017	36.67	0.48
0.0003	0.00022	18.33	0.286
0.0004	0.00017	40	0.92
0.0006	0.00020	30	0.87
0.0010	0.00040	20	0.48
$y = 718.37x + 0.09$, $F_{1,8df} = 3.66$, $(P > F) = 0.09$[b]			
$m = 5.77p + 6.02$, $F_{1,8df} = 1.05$, $(P > F) = 0.34$[c]			
	Medium Larvae		
0.0001	0.00008	26.67	0.44
0.0002	0.00017	15	0.16
0.0002	0.00012	25	0.40
0.0002	0.00010	13.33	0.23
0.0002	0.00014	21.67	0.29
0.0002	0.00017	61.67	0.80
0.0003	0.00022	0	0
0.0004	0.00017	28.33	0.65

Table 40. continued.

Prey density (per cm^2)[a]	Predator density (per cm^2)[b]	Predator-induced mortality (%)	No. of prey consumed per predator
	Medium Larvae		
0.0006	0.00020	0	0
0.0010	0.00040	26.67	0.64
$y = 139.46\ x + 0.31$, $F_{1,8df} = 0.15$, $(P > F) = 0.71$[b]			
$m = -0.74p + 23.14$, $F_{1,8df} = 0.01$, $(P > F) = 0.92$[c]			

[a] Leaf area estimates can be found in Appendix C.

[b] y = number of prey consumed per predator; x = prey density

[c] m = predator-induced mortality; p = predator density

Table 41. The response of the predator complex to changes in the density of small velvetbean caterpillar larvae released at Green Acres in 1982 and the response of the predator complex to changes in predator density. The values are ranked in order of increasing prey density.

Prey density (per cm^2)[a]	Predator density (per cm^2)[a]	Predator-induced mortality (%)	No. of prey consumed per predator
0.0001	0.00010	14.28	0.192
0.0001	0.00006	13.34	0.31
0.0001	0.00006	24.44	0.48
0.0001	0.00009	66.67	0.95
0.0002	0.00010	12	0.19
0.0002	0.00006	16	0.55
0.0002	0.00015	27.78	0.38
0.0003	0.00003	17,14	1.50
0.0008	0.00007	48.57	5.67
0.0010	0.00005	38	7.6

$y = 7545.17x - 0.62$, $F_{1,9df} = 90.26$, $(P > F) = 0.0001$[b]

$m = 2.15p + 26.29$, $F_{1,9df} = 0.01$, $(P > F) = 0.92$[c]

[a] Leaf area estimates can be found in Appendix C.

[b] y = number of prey consumed per predator; x = prey density

[c] m = predator-induced mortality; p = predator density

($P > 0.05$) among years. This suggests that, at least for 1980-1982, the density of alternate lepidopterous prey had little or no effect on the mortality inflicted by a predator complex on VBC larvae.

The second hypothesis of the inconsistency of the response by the predator complex to prey density is that the species composition of the predator complex in association with the densities of each species comprising the complex are critical in determining the response of the predator complex as has been shown in greenhouse and field cage studies (van den Bosch et al. 1969, Tamaki and Weeks 1972b, Barry et al. 1974). This hypothesis suggests that the species composition and the densities of each species comprising the complex in 1980 and 1982 were such that the complex was able to respond functionally to changes in prey density. This hypothesis appears implausible because the predator complexes found within the field in 1980-1982 were similar in composition (Tables 8, 14, 27, 33; Appendix B) and density (Table 14; Appendix B). However, the sampling techniques used to determine composition and density of the predator complex were not sensitive enough to provide the information necessary to adequately test this hypothesis. In addition, the data from the Archer field suggested that more than 1 predator complex could demonstrate the same response. Therefore, more rigorous testing is required to determine the importance of the composition and density of the species comprising the predator complex on the amount of mortality inflicted on prey populations by the predator complex.

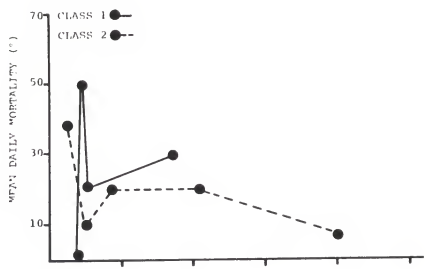
To investigate the effect of increases in leaf area on predation mortality further, the response of the predator complex to changes

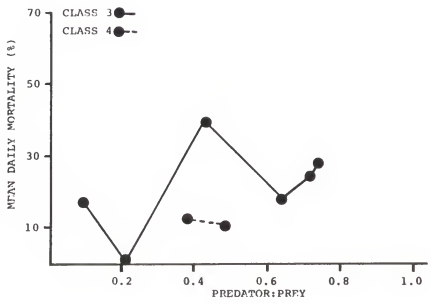
in predator population densities was investigated by regressing the predator-induced mortality on the mean total predators per unit leaf area (cm^2). For each stage and year, no significant relationships of predator-induced mortality with predator density were found (Tables 39-41). This suggests that there was no simple, linear relationship between the amount of mortality inflicted by a predator complex and the density of all species comprising the complex.

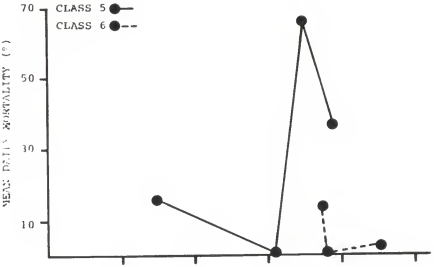
To complete the investigation of the effect of leaf area on predation mortality requires examination of the response of the predator complex to changes in both prey and predator population densities. This response can be elucidated by examining the patterns of predator-induced mortality associated with the ratios of predator to prey densities for each leaf area. To facilitate examination of the patterns, the data from all years were combined for each stage of larvae and the leaf area of plants was classified into 1 of 8 leaf area classes. The leaf area classes represented incremental increases in leaf area of 10,000 cm^2 (e.g., class 1 = 1-10,000 cm^2, class 2 = 10,001-20,000 cm^2, and so on).

The pattern of predator-induced mortality associated with the predator-prey ratio for both small and medium larvae was non-linear. The predator-induced mortality was greatest at one predator-prey ratio in each leaf area class and decreased in both directions from this predator-prey ratio (Figures 14-15). As expected, the value of the predator-prey ratio at which maximum predation mortality occurred increased with leaf area (Figures 14-15). The maximum amount of mortality associated with each of these ratios, however,

Figure 14. The relationship between predator-prey ratio and the mean daily predator-induced mortality at each leaf area class for small velvetbean caterpillar larvae at Green Acres, 1980-1982. The leaf area classes are based on incremental increases in leaf area of 10,000cm^2 (e.g., class 1 = 1-10,000 cm^2, class 2 = 10,001-20,000 cm^2, and so on).


CLASS 1
CLASS 2
70
50
30
10


CLASS 3
CLASS 4
MEAN DAILY MORTALITY (%)
70
50
30
10
0.2
0.4
0.6
0.8
1.0
PREDATOR:PREY


CLASS 5
CLASS 6
70
50
30
10

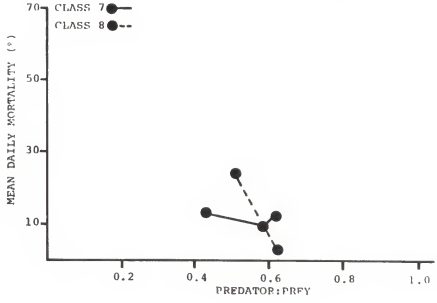
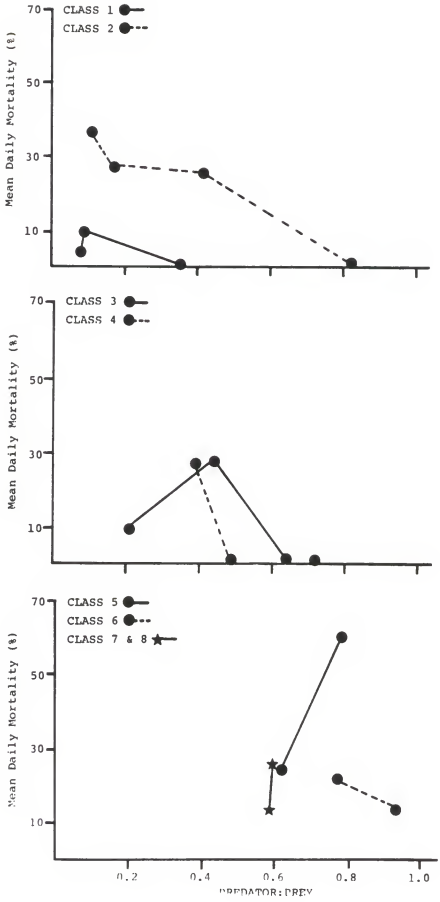

CLASS 7
CLASS 8
MEAN DAILY MORTALITY (%)
70
50
30
10
0.2
0.4
0.6
0.8
1.0
PREDATOR:PREY

Figure 15. The relationship between the predator-prey ratio and the mean daily predator-induced mortality at each leaf area class for medium velvetbean caterpillar larvae at Green Acres, 1980-1982. The leaf area classes are based on incremental increases in leaf area of 10,000 cm^2 (e.g., class 1 = 1-10,000 cm^2, class 2 = 10,001-20,000 cm^2, and so on).


CLASS 1
CLASS 2
Mean Daily Mortality (%)
70
50
30
10
CLASS 3
CLASS 4
Mean Daily Mortality (%)
70
50
30
10
CLASS 5
CLASS 6
CLASS 7 & 8
Mean Daily Mortality (%)
70
50
30
10
0.2
0.4
0.6
0.8
1.0
PREDATOR:PREY

gradually decreased with an increase in leaf area for the small larvae, and remained relatively constant over all leaf area classes for medium larvae (Figures 14-15). This suggests that the amount of mortality inflicted upon a prey population by a predator complex is dependent upon both the leaf area and the predator-prey ratio. The maximum amount of mortality expected from a predator-prey ratio for a particular leaf area class will depend upon the species composition of the predator complex and the density of each species comprising the complex.

To represent the slight or no response of the predator complex in the initial multipredator-VBC model requires that the significant effect of leaf area on the preator response be considered. This can be accomplished by representing the predator-induced mortality associated with various predator-prey ratios in each leaf area category by a mortality curve that increases at a decreasing rate, reaching an initial plateau equal to some maximum predation mortality. This maximum mortality would occur at one predator-prey ratio for a given leaf area class. For predator-prey ratios greater than this, the mortality curve would decrease to a lower, constant level of mortality that would represent the effects of interference among predator species within the complex. The value of the mortality at each plateau and the predator-prey ratio at which these plateaus occur would be characteristic for a particular predator complex.

In conclusion, the response of the predator complex cannot be described simply by changes in the densities of prey and predator

populations. The predator response is influenced by the tremendous increase in leaf area that occurs early to midseason. The predator species comprising the complex must respond to changes in leaf area by changing their searching behavior in order for the complex to increase the mortality inflicted on a prey population as predator population densities increase. Such changes in searching behavior are required so that the predators can maintain their searching efficiency and continue to capture and consume a constant proportion of prey.

Notes

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CONCLUSIONS

The method utilized for quantifying arthropod predation on VBC eggs and larvae provided the information required to make first approximations in the quantitative assessment of the role of arthropod predation in prey population dynamics. This step required estimates of the stage specific mortality inflicted by all predators and identification of the species responsible for that mortality. The method provided this information by providing a means by which estimates of total mortality could be partitioned according to predator species.

From the results obtained by using the method to estimate predation rates on small and medium VBC larvae, the impact of arthropod predation on VBC dynamics at Green Acres in 1980-1982 was assessed. For each year and stage, the mortality inflicted by the arthropod predator complex appeared to remain constant or decrease as the season progressed (Figures 3, 4, 10, 11, 13). These near constant rates of mortality were maintained despite changes in prey density, predator density (Table 14; Appendix B), and leaf area (Appendix C). When examining the response of the predator complexes to the individual components of prey density and predator density, no significant responses were

found, except for the significant, positive, linear response demonstrated by the predator complexes present in 1980 and 1982 to changes in the density of small VBC larvae (Tables 39, 41). These responses appear inconsistent with the constant rates of mortality, but can be reconciled with the constant rates by considering the changes in leaf area that occurred as the season progressed. These increases in leaf area in early to midseason may have overridden the responses of the predator complexes, causing the slightly dampened mortality rates. These dampened mortality rates in combination with recruitment into the VBC populations through an influx of VBC adults and/or an increase in fecundity of adult females, may have resulted in a loss of regulation of VBC populations by arthropod predators. To explain this overriding influence of leaf area on the response of the predator complex satisfactorily, however, will require further investigation.

The increases in leaf area that occurred in early to midseason increased the spatial heterogeneity of the universe searched by arthropod predators. Such increases in spatial heterogeneity have been shown to increase the stability of predator-prey interactions when the spatial heterogeneity was maintained for a period of time at an increased level (Huffaker 1958, Huffaker et al. 1963, Murdoch and Oaten 1975). However, in the Green Acres field in 1980-1982, the predator-VBC interaction was unstable as was evident from the large densities of VBC larvae that occurred each year (Table 14; Appendix B). This suggests that the stability imparted by spatial heterogeneity may depend

upon either the amount of spatial heterogeneity within a system, the rate at which spatial heterogeneity is changing, or some combination of these factors. Experiments specifically designed to investigate each of these factors and their effect on the stability of predator-prey interactions need to be conducted.

The results obtained from using the method presented in this study to estimate predation rates on VBC eggs and larvae demonstrated the flexibility of the method for use on more than 1 life stage of prey. To make the method generally applicable for estimating predation rates of immature life stages of noctuid pests of row crops, however, will require some refinements in the techniques. These refinements include estimation of the mortality rates associated with a range of prey densities, estimates of mortality with a finer time resolution than once a week, and techniques for partitioning total mortality estimates according to the habitat where predation occurred (foliage or ground) and for identifying all predator species responsible for the predator-induced mortality.

The first refinement of the technique is necessary because the estimates of total, large field cage, and background mortality determined in this study, were assumed to represent an average value of mortality for the range of prey densities that occur within the field. The estimates, however, may not have been representative of such average values because they were determined for only 1 prey density each week. To estimate this average value of mortality, the mortality rates associated with a series of prey densities should be estimated each week. In addition to estimating a representative average value of mortality, the

series of mortality estimates will allow examination of the effects of changes in prey density on predator-induced mortality without the confounding effects of changes in leaf area and predator density.

The second refinement of the method, mortality estimates with a finer time resolution than weekly, is required because weather conditions can change dramatically from day to day (even within a day), and these changes may influence the activity of predators and VBC (e.g., effect of temperature on predator foraging behavior, Tables 12, 13, 31, 32, 37, 38; effect of rain on the frequency of fall of small VBC larvae, Table 25). Some changes in weather conditions may reduce the predation pressure exerted on VBC populations and may act as a "refuge" for VBC. The timing of these weather refugia may contribute to the loss of VBC population regulation by arthropod predators. With estimates of predator-induced mortality with a finer time resolution (e.g., every 2 days during the season), the effects of various weather conditions on the amount of predator-induced mortality inflicted on VBC populations can be investigated.

The third refinement of the mark-release-recapture technique is necessitated by the inflated estimates of ground predator mortality obtained from the releases of prey made into the large field cage. The inflated estimates were due to the relaxation of the competition between ground and foliage predators for prey. To alleviate this problem, the technique may be modified by eliminating the releases with the estimation of 2 frequencies: the frequency with which prey fall to the ground, and the

frequency with which prey are captured and consumed once on the ground. The mortality occurring on the ground may then be estimated by the appropriate combination of these 2 frequencies with estimates of the densities of predator and prey populations.

The final refinement of the method is required to insure that all predator species responsible for the mortality are identified and that an adequate number of observations are recorded, so that the predator-induced mortality can be partitioned according to predator species. The direct observation technique appeared to identify only those predators that were not disturbed by the presence of the observer and/or remained at the site of capture for a period of time to consume prey. In addition, the number of predation events observed using the direct observation technique was not sufficient to partition the estimates of predator-induced mortality according to species. To identify those predators that are disturbed by the presence of the observer and/or do not remain at the site of capture for a period of time, and to increase the number of observations of predation events, another technique such as an ELISA should be used. The ELISA technique is particularly useful because the arthropod predators preying upon a particular prey species can be identified without the introduction of marked laboratory reared larvae, provided that specific antisera and adequate sampling techniques are available. Ideally, the other technique should be used simultaneously with the direct observation technique, and the results from both techniques compared. The technique that identifies the

most predator species and provides the largest number of records of predation events should be incorporated into the method.

Incorporation of these refinements should result in a general method for quantitative estimation of rates of arthropod predation on immature life stages of a single or a complex of noctuid pests in row crops. The techniques can be modified for use with a complex of pests by substituting individuals of the various species comprising the prey complex in the proportions they occur in the field for the individuals of a single species in the mark-release-recapture and direct observation techniques. The use of the method with a complex of pests should provide some insight into the mechanisms of predator switching and prey preference.

From the use of the method, an initial assessment of the role of arthropod predators in pest population dynamics can be made. This assessment represents the first step in the effective utilization of arthropod predators in pest management programs. From this first step, the many factors that influence the impact of arthropod predators, such as leaf area and species composition of the predator complex, can be investigated. The results from such investigations should provide the information required to predict the impact of a given predator complex on the dynamics of a pest population and to maintain or enhance the mortality inflicted on a pest population by a predator complex in a management program.

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APPENDIX A
SUMMARY OF FIELD TEMPERATURES - 1980-1982

Table A1. Summary of temperature (canopy) data from Green Acres, 1980. (°C)

Date	Upper		Middle		Lower	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
July 14	22.8	37.9	22.9	38.5	23.3	38.2
July 21	22.4	36.8	22.6	38.4	23.1	37.0
July 28	21.8	34.1	21.7	33.0	22.1	31.8
August 4	19.7	41.0	20.5	35.7	20.6	33.1
August 11	20.4	39.5	21.1	39.3	21.0	36.4
August 18	23.0	36.8	23.0	34.1	23.3	32.3
August 25	17.5	30.4	17.4	28.9	18.3	28.6
September 1	19.1	32.6	19.5	30.7	19.8	29.9
September 8	18.0	37.9	18.1	36.6	18.3	37.7
September 15	19.2	39.2	19.1	40.1	19.3	39.1
September 22	20.4	37.3	20.4	37.9	20.7	37.2

Table A2. Summary of the ambient temperatures at Archer, 1980. (°C)

Date	Minimum	Maximum
July 9	23.9	34.4
July 16	22.2	36.1
July 23	21.7	31.1
August 6	20.6	34.4
August 13	22.8	30.6
August 20	22.5	33.3
August 27	20.6	33.3

Table A3. Summary of the canopy and soil temperatures at Green Acres, 1981. (°C)

Date	Soil		Upper		Middle		Lower	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
July 14	25.7	34.7	24.3	40.2	24.3	40.4	24.3	43.7
July 21	24.3	32.4	23.1	32.1	23.1	32.0	22.9	32.8
July 28	20.2	54.6	20.7	43.5	20.5	42.2	20.4	42.4
August 4	21.4	31.6	19.0	34.3	19.0	34.6	19.0	34.2
August 11	23.4	32.5	21.4	33.5	21.4	34.9	21.4	31.2
August 18	23.7	29.4	22.4	31.5	22.3	33.8	22.2	32.6
August 25	21.2	28.5	17.8	31.5	17.6	33.2	17.6	36.2
September 1	22.1	28.6	18.7	32.2	18.6	35.9	18.3	44.0
September 8	21.7	29.7	19.4	33.3	19.2	36.4	19.0	41.8
September 15	20.7	30.7	17.7	36.8	17.5	40.4	17.0	36.7
September 22	18.8	26.5	15.5	32.4	15.4	34.1	15.3	37.3

Table A4. Summary of the canopy and soil temperatures for Green Acres, 1982, (°C)

Date	Soil		Upper		Middle		Lower	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
July 6	22.0	45.6	-	-	-	-	-	-
July 13	23.9	32.5	20.5	39.9	-	-	20.5	36.0
July 20	22.9	30.9	22.1	36.3	-	-	19.9	35.2
July 27	24.3	27.5	22.8	27.1	23.1	27.4	23.4	26.9
August 3	22.8	30.6	20.8	32.1	20.7	32.3	20.6	33.0
August 10	22.6	36.3	21.2	36.6	21.4	35.8	21.6	34.1
August 17	21.7	30.2	20.3	33.8	20.5	32.1	20.2	31.1
August 24	22.3	30.1	20.6	36.0	21.2	53.2	21.5	31.5
August 31	20.0	32.9	17.7	33.2	17.7	34.1	18.2	32.1
September 7	20.2	28.8	17.2	33.0	17.6	32.9	18.1	31.1
September 14	22.4	29.7	21.2	33.8	21.3	39.1	21.7	33.1

APPENDIX B
SUMMARY OF THE POPULATION DENSITIES OF
PREDATORS AND VELVETBEAN CATERPILLAR LARVAE - 1980-1982

Table B1. Summary of the density of lepidopterous and velvetbean caterpillar larvae (variance) at Green Acres (GA) and Archer (AR), 1980. (Mean number/91 cm row)

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
June 30 - July 2						
GA	0 (+)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
AR	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 7 - July 9						
GA	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
AR	0.3 (0.5)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 14 - July 16						
GA	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0 (-)	0 (-)
AR	0.1 (0.1)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 21 July 23						
GA	0 (-)	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0.2 (0.2)
AR	----------	----------	Rain	----------	----------	----------

Table B1. continued.

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
July 28 - July 30						
GA	0.2	0	0.2	0	0	0
	(0.2)	(-)	(0.2)	(-)	(-)	(-)
AR	0.8	0	0	0	0.5	0
	(0.7)	(-)	(-)	(-)	(0.6)	(-)
August 4 - August 6						
GA	0.2	0	0	0.2	0	0
	(0.2)	(-)	(-)	(0.2)	(-)	(-)
AR	0.9	0.4	0.1	2.9	0.4	0.4
	(0.6)	(0.3)	(0.1)	(5.0)	(0.6)	(0.3)
August 11 - August 13						
GA	0	0.2	0	3.4	1.8	0.8
	(-)	(0,2)	(-)	(4.3)	(0.2)	(0.7)
AR	0.8	0.4	0.1	10.25	3.9	2.1
	(0.9)	(0.6)	(0.1)	(19.64)	(5.3)	(5.3)
August 18 - August 20						
GA	0	0	0.4	8.6	3.0	3.6
	(-)	(-)	(0.8)	(10.8)	(1.0)	(4.8)
AR	0.5	0.4	0.3	0.9	0.1	0.1
	(0.6)	(0.3)	(0.2)	(2.1)	(0.1)	(0.1

Table B1. continued.

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
August 25 - August 27						
GA	0 (-)	0 (-)	0.2 (0.2)	18.6 (49.3)	6.2 (3.7)	5.6 (2.3)
AR	2.3 (3.1)	0.8 (0.6)	0.4 (0.6)	29.3 (115.9)	3.3 (5.1)	0.1 (0.1)
September 1						
GA	0.2 (0.02)	0 (-)	0 (-)	35.8 (187.2)	52.2 (1356.7)	25.8 (238.7)
September 8						
GA	0 (-)	0 (-)	0 (-)	8.2 (21.2)	27.6 (89.3)	34.2 (163.2)
September 15						
GA	0.2 (0.2)	0 (-)	0 (-)	2.6 (13.8)	7.6 (8.8)	3.6 (10.8)
September 22						
GA	0 (-)	0.2 (0.2)	0 (-)	1.0 (3.0)	0.4 (0.5)	0.6 (0.8)

[a]Small = length < 12.5 mm; Medium = length 12.5 mm - 25 mm; Large = length > 25mm.

Table B2. Summary of the predator population densities (variance) at Green Acres, 1981. (Mean number/91 cm row)

Date	Total	Clubionidae	Thomisidae	*Peucetia viridans* (H.)	Salticidae	*Oxyopes salticus* H.	Small Spiders	Lycosidae	Other Spiders	Formicidae	Carabidae
July 7											
Morning	2.2	0	0	0	0	0	0	0	0	0.2	0
	(1.0)	(-)	(-)	(-)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)
Afternoon	0.8	0	0	0	0	0	0.2	0	0	0	0
	(0.5)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)	(-)	(-)	(-)
July 14											
Morning	1.8	0	0	0	0	0.4	0.2	0	0	0	0
	(0.7)	(-)	(-)	(-)	(-)	(0.2)	(0.2)	(-)	(-)	(-)	(-)
Afternoon	2.2	0	0	0	0	0	0.2	0	0	0	0
	(0.6)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)	(-)	(-)	(-)
Evening	1.2	0	0	0	0.2	0	0	0	0	0	0
	(0.7)	(-)	(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)
July 21											
Morning	4.4	0	1.2	0	0	0.2	0	0	0	0.2	0
	(1.5)	(-)	(1.0)	(-)	(-)	(0.2)	(-)	(-)	(-)	(0.2)	(-)
Afternoon	4.8	0	0	0	0.2	0	0.2	0	0	0	0
	(1.0)	(-)	(-)	(-)	(0.2)	(-)	(0.2)	(-)	(-)	(-)	(-)
Evening	3.4	0	0	0	0.2	0	0	0	0	0.6	0
	(2.8)	(-)	(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(0.8)	(-)
July 28											
Morning	5.2	0	0.2	0	0	0	0.4	0	0	0	0
	(0.8)	(-)	(0.2)	(-)	(-)	(-)	(0.2)	(-)	(-)	(-)	(-)
Afternoon	3.8	0	0	0	0	0	0.2	0	0.2	0	0
	(1.1)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)	(0.2)	(-)	(-)
Evening	4.0	0	0.2	0	0	0	0	0	0	0.4	0
	(5.5)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)	(0.8)	(-)

Coccinellidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus Reuter	Reduviidae
0	0	0	0	1.4	0	0.6	0	0	0
(-)	(-)	(-)	(-)	(0.7)	(-)	(0.4)	(-)	(-)	(-)
0	0	0.2	0	0	0	0	0	0.4	0
(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)
0	0	0.4	0	0.4	0	0	0	0.4	0
(-)	(-)	(0.3)	(-)	(0.3)	(-)	(-)	(-)	(0.3)	(-)
0	0	0.8	0	0.8	0	0	0	0.4	0
(-)	(-)	(0.7)	(-)	(0.4)	(-)	(-)	(-)	(0.8)	(-)
0	0	0.8	0	0.2	0	0	0	0	0
(+)	(-)	(0.7)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)
0	0	0.6	0	1.2	0	0	0.2	0.8	0
(-)	(-)	(0.3)	(-)	(0.4)	(-)	(-)	(0.2)	(0.7)	(-)
0	0	0.6	0	1.2	0	0	0.2	2.4	0
(-)	(-)	(0.8)	(-)	(0.4)	(-)	(-)	(0.2)	(3.3)	(-)
0	0	1.2	0	1.0	0	0	0	0.4	0
(-)	(-)	(1.7)	(-)	(2.0)	(-)	(-)	(-)	(0.3)	(-)
0	0	1.4	0	1.0	0	0	1.4	0.8	0
(-)	(-)	(0.6)	(-)	(0.6)	(-)	(-)	(0.8)	(0.4)	(-)
0	0	1.4	0	1.0	0.2	0	0.2	0.4	0
(-)	(-)	(1.3)	(-)	(0.6)	(0.2)	(-)	(0.2)	(0.3)	(-)
0	0	0.6	0	0	0	0	0.4	2.4	0
(-)	(-)	(0.8)	(-)	(-)	(-)	(-)	(0.3)	(10.3)	(-)

Table B2. continued.

Date	Total	Clubionidae	Thomisidae	Peucetia viridans (H.)	Salticidae	Oxyopes salticus H.	Small Spiders	Lycosidae	Other Spiders	Formicidae	Carabidae
August 4											
Morning	4.6	0	0	0	0.2	0	0.4	0	0	0	0
	(0.8)	(-)	(-)	(-)	(0.2)	(-)	(0.4)	(-)	(-)	(-)	(-)
Afternoon	8.2	0	0	0	0	0	2.0	0	0.2	0.4	0
	(2.3)	(-)	(-)	(-)	(-)	(-)	(1.8)	(-)	(0.2)	(0.4)	(-)
Evening	----------	----------	----------	----------	----------	----------	Rain	----------	----------	----------	----------
August 11											
Morning	7.0	0	0	0	0	0	1.2	0	0	0.4	0
	(1.7)	(-)	(-)	(-)	(-)	(+)	(0.4)	(-)	(-)	(0.3)	(-)
Afternoon	8.4	0	0	0	0.2	0	0.6	0	0.4	0	0.2
	(1.3)	(-)	(-)	(-)	(0.2)	(-)	(0.4)	(-)	(0.3)	(-)	(0.2)
Evening	----------	----------	----------	----------	----------	----------	Rain	----------	----------	----------	----------
August 18											
Morning	11.4	0	0.2	0	0	0.6	0.6	0	0	0.2	0
	(2.6)	(-)	(0.2)	(-)	(-)	(0.6)	(0.4)	(-)	(-)	(0.2)	(-)
Afternoon	8.6	0.2	0.2	0.2	0	0.2	1.0	0	0	2.6	0.2
	(1.9)	(0.2)	(0.2)	(0.2)	(-)	(0.2)	(0.8)	(-)	(-)	(1.9)	(0.2
Evening	2.6	0.2	0.2	0	0.2	0	0	0	0	0	0
	(3.3)	(0.2)	(0.2)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)
August 25											
Morning	7.2	0	0	0.2	0	0.2	0.8	0	0.4	0	0.2
	(1.2)	(-)	(-)	(0.2)	(-)	(0.2)	(0.2)	(-)	(0.2)	(-)	(0.2)
Afternoon	5.6	0	0	0	0	0.6	0.6	0	0	0.2	0
	(2.2)	(-)	(-)	(-)	(-)	(0.2)	(0.4)	(-)	(-)	(0.2)	(-)
Evening	4.6	0	0	0.2	0.2	0	0	0	0	0	0.2
	(2.8)	(-)	(-)	(0.2)	(0.2)	(-)	(-)	(-)	(-)	(-)	(0.2)

Coccinellidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus (Reuter)	Reduviidae
0	0	1.6	0	0.8	0.2	0	1.4	1.6	0
(-)	(-)	(2.3)	(-)	(0.4)	(0.2)	(-)	(0.7)	(1.3)	(-)
0	0	1.6	0	0.6	1.2	0	0.2	0.4	0
(-)	(-)	(2.3)	(-)	(0.4)	(0.6)	(-)	(0.2)	(0.8)	(-)
Rain									
0	0	1.6	0	0.4	0.8	0	1.8	0.6	0
(-)	(-)	(1.3)	(-)	(0.2)	(0.4)	(-)	(4.2)	(0.8)	(-)
0	0	2.4	0.4	0.8	1.0	0	1.6	0.8	0
(-)	(-)	(2.8)	(0.2)	(0.5)	(0.5)	(-)	(2.3)	(0.2)	(-)
Rain									
0	0.2	4.8	0	1.8	0.2	0.2	1.6	0.6	0.4
(-)	(0.2)	(6.7)	(-)	(0.9)	(0.2)	(0.2)	(1.3)	(0.4)	(0.2)
0	0.2	1.4	0	0.4	0	0	2.0	0	0
(-)	(0.2)	(0.3)	(-)	(0.2)	(-)	(-)	(4.0)	(-)	(-)
0	0.2	0.2	0	0.6	0	0.6	0.2	0.2	0
(-)	(0.2)	(0.2)	(-)	(0.3)	(-)	(1.8)	(0.2)	(0.2)	(-)
0	0	1.8	0	0.2	0	0.8	0.6	0.2	0.6
(-)	(-)	(3.7)	(-)	(0.2)	(-)	(0.8)	(0.3)	(0.2)	(0.6)
0	0	1.2	0.2	1.0	0	0.2	2.0	0.4	0.4
(-)	(-)	(1.2)	(0.2)	(0.6)	(-)	(0.2)	(3.5)	(0.2)	(0.2)
0	0	0.6	0	2.0	0	0.8	0	0.4	0
(-)	(-)	(0.3)	(-)	(2.5)	(-)	(1.7)	(-)	(0.3)	(-)

Table B2. continued.

Date	Total	Clubionidae	Thomisidae	Peucetia viridans (H.)	Salticidae	Oxyopes salticus H.	Small Spiders	Lycosidae	Other Spiders	Formicidae	Carabidae
September 1											
Morning	6.6	0.4	0	0	0	0.4	1.6	0	0.2	0.8	0
	(0.9)	(0.2)	(-)	(-)	(-)	(0.2)	(0.5)	(-)	(0.2)	(0.5)	(-)
Afternoon	6.4	0.4	0	0	0.2	0	0.8	0	0	0	0
	(1.0)	(0.4)	(-)	(-)	(0.2)	(-)	(0.4)	(-)	(-)	(-)	(-)
Evening	5.0	0	0	0.2	0.4	0	1.4	0	0	0	0
	(1.5)	(-)	(-)	(0.2)	(0.3)	(-)	(4.3)	(-)	(-)	(-)	(-)
September 8											
Morning	10.4	1.0	0	0.4	0.2	0.2	0.6	0.2	0	0.6	0.4
	(2.5)	(0.5)	(-)	(0.4)	(0.2)	(0.2)	(0.6)	(0.2)	(-)	(0.4)	(0.2)
Afternoon	10.6	0.6	0.2	0	0.2	0.2	1.0	0	0.2	0.2	0.2
	(2.5)	(0.2)	(0.2)	(-)	(0.2)	(0.2)	(0.3)	(-)	(0.2)	(0.2)	(0.2)
Evening	6.4	0.8	0	0	0	0	0.6	0	0	0	0
	(10.3)	(0.2)	(-)	(-)	(-)	(-)	(0.8)	(-)	(-)	(-)	(-)
September 15											
Morning	13.8	0.8	0.2	0	0.4	0	0.4	0.2	0.4	2.4	0
	(1.9)	(0.6)	(0.2)	(-)	(0.2)	(-)	(0.2)	(0.2)	(0.2)	(2.4)	(-)
Afternoon	9.0	0.2	0	0	0	0	1.2	0.2	0.2	0	0.2
	(2.3)	(0.2)	(-)	(-)	(-)	(-)	(0.7)	(0.2)	(0.2)	(-)	(0.2)
Evening	4.2	0.4	0.2	0	0	0	0.2	0	0	0	0
	(3.2)	(0.3)	(0.2)	(-)	(-)	(-)	(0.2)	(-)	(-)	(-)	(-)
September 22											
Morning	7.6	0.4	0.2	0	1.0	0	0.6	0.4	0	0.2	0.2
	(1.1)	(0.2)	(0.2)	(-)	(0.5)	(-)	(0.4)	(0.4)	(-)	(0.2)	(0.2)
Afternoon	6.8	0	0	0	0.8	0.2	0.6	0.2	0	0	0
	(1.0)	(-)	(-)	(-)	(0.4)	(0.2)	(0.4)	(0.2)	(-)	(-)	(-)
Evening	3.8	0	0	0	0.2	0.4	0	0	0.2	0	0
	(4.2)	(-)	(-)	(-)	(0.2)	(0.3)	(-)	(-)	(0.2)	(-)	(-)

Coccinellidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus (Reuter)	Reduviidae
0	0.2	0.6	0	0.4	0.2	0	1.8	0	0
(-)	(0.2)	(0.3)	(-)	(0.2)	(0.2)	(-)	(3.2)	(-)	(-)
0	0	1.6	0	1.2	0	0	2.0	0.2	0
(-)	(-)	(0.8)	(-)	(0.4)	(-)	(-)	(0.5)	(0.2)	(-)
0	0	1.0	0	0.4	0	0.4	0.8	0.2	0.2
(-)	(-)	(3.0)	(-)	(0.3)	(-)	(0.8)	(1.7)	(0.2)	(0.2)
0	0.2	2.6	0	0.6	0	0	3.2	0.2	0
(-)	(0.2)	(3.8)	(-)	(0.4)	(-)	(-)	(9.7)	(0.2)	(-)
0	0	2.4	0	0.2	0	2.2	2.8	0.2	0
(-)	(-)	(3.8)	(-)	(0.2)	(-)	(19.2)	(6.2)	(0.2)	(-)
0	0	0.6	0	0.4	0	1.4	1.8	0.8	0
(-)	(-)	(0.8)	(-)	(0.3)	(-)	(9.8)	(1.7)	(3.2)	(-)
0	0	5.6	0	0	0	0	3.2	0.2	0
(-)	(-)	(4.3)	(-)	(-)	(-)	(-)	(4.7)	(0.2)	(-)
0	0	3.0	0	0	0	0	3.8	0	0.2
(-)	(-)	(2.5)	(-)	(-)	(-)	(-)	(8.2)	(-)	(0.2)
0	0	2.0	0	0.6	0	0	0.6	0	0
(-)	(-)	(0.5)	(-)	(0.8)	(-)	(-)	(0.8)	(-)	(-)
0	0	2.4	0	0	0	0.2	1.8	0	0
(-)	(-)	(0.8)	(-)	(-)	(-)	(0.2)	(1.7)	(-)	(-)
0	0	3.4	0	0	0	0	1.6	0	0
(-)	(-)	(2.8)	(-)	(-)	(-)	(-)	(1.3)	(-)	(-)
0	0.2	1.6	0	0.4	0	0.2	0.6	0	0
(-)	(0.2)	(0.8)	(-)	(0.3)	(-)	(0.2)	(0.3)	(+)	(-)

Table B3. Summary of the activities and densities of ground predators (variance) at Green Acres, 1981.[a]

Species	July				August					September		
	7	14	21	28	4	11	18	25	1	8	15	22
Labidura riparia (Pallas) adult	4.6 (10.9)	1.3 (2.8)	1.5 (2.7)	1.5 (1.8)	2.5 (10.7)	1.5 (3.3)	4.2 (12.1)	4.6 (17.1)	9.5 (37.3)	9.6 (34.8)	12.3 (30.9)	18.1 (117.4)
Labidura riparia (Pallas) nymph	3.5 (8.3)	1.4 (1.9)	6.6 (18.9)	2.2 (3.9)	0.4 (0.4)	3.1 (10.2)	7.7 (26.6)	9.7 (50.0)	14.9 (87.0)	14.1 (38.7)	17.5 (57.5)	34.0 (135.2)
Pheidole morrisi Forel	0.2 (0.1)	0.3 (0.3)	0.5 (1.1)	0.1 (0.1)	–	0.2 (0.4)	0.7 (1.6)	0.3 (0.6)	–	0.3 (0.8)	0.1)0.1)	0.2 (0.3)
Pardosa spp.	0.1 (0.1)	0.1 (0.1)	0.2 (0.3)	0.1 (0.1)	–	0.1 (0.1)	–	0.1 (0.1)	0.6 (0.9)	1.1 (1.1)	0.4 (0.5)	0.5 (0.5)
Pheidole dentata Mayr	–	0.1 (0.1)	0.3 (0.6)	3.9 (22.5)	–	0.3 (0.6)	3.1 (34.5)	3.4 (27.6)	3.4 (113)	4.5 (106)	2.9 (36.6)	0.6 (1.5)
Calosoma spp.	–	–	–	–	–	–	0.1 (0.1)	0.2 (0.2)	0.1 (0.1)	0.7 (1.1)	1.3 (2.8)	0.7 (1.4)
Lycosidae	–	–	–	–	–	–	–	0.4 (0.4)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.2 (0.2)
Solenopsis geminata (F.)	–	0.1 (0.1)	–	–	0.1 (0.1)	–	–	–	–	3.9 (215)	13.2 (2137)	2.2 (45.9)

[a]Mean number/20 traps

Table B4. Summary of the densities of other lepidoptera larvae and velvetbean caterpillar larvae (variance) at Green Acres, 1981. (Mean number/91 cm row)

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
July 7						
Morning	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Afternoon	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 14						
Morning	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Afternoon	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Evening	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 21						
Morning	1.8 (6.2)	0 (-)	0 (-)	0.2 (0.2)	0 (-)	0 (-)
Afternoon	1.6 (0.6)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Evening	0 (-)	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0 (-)

Table B4. continued.

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
August 18						
Morning	1.2 (3.2)	2.2 (3.2)	0 (-)	1.8 (0.7)	1.2 (0.8)	0 (-)
Afternoon	0.2 (0.2)	0 (-)	0.4 (0.8)	2.0 (0.8)	0.4 (0.2)	0.4 (0.2)
Evening	0 (-)	0 (-)	0 (-)	1.2 (1.7)	0.4 (0.3)	0 (-)
August 25						
Morning	0 (-)	0.2 (0.2)	0.2 (0.2)	1.6 (0.7)	1.0 (0.3)	0 (-)
Afternoon	0 (-)	0 (-)	0 (-)	3.0 (1.0)	1.4 (0.7)	1.4 (0.4)
Evening	0 (-)	0 (-)	0.2 (0.2)	1.2 (0.7)	0.8 (1.7)	0.2 (0.2)
September 1						
Morning	0 (-)	0 (-)	0.2 (0.2)	2.6 (0.7)	3.0 (0.6)	3.6 (0.7)
Afternoon	0 (-)	0.2 (0.2)	0 (-)	2.6 (1.5)	2.6 (1.4)	2.4 (0.9)
Evening	0 (-)	0 (-)	0.2 (0.2)	1.4 (1.3)	1.4 (0.8)	0.6 (0.3)

Table B4. continued.

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
July 28						
Morning	1.2 (1.2)	0 (-)	0 (-)	0.2 (0.2)	0 (-)	0 (-)
Afternoon	0.6 (0.2)	0.2 (0.2)	0 (-)	0 (-)	0.2 (0.2)	0 (-)
Evening	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
August 4						
Morning	0.2 (0.2)	0.2 (0.2)	0 (-)	0.2 (0.2)	0.4 (0.2)	0 (-)
Afternoon	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Evening	----------	----------	Rain	----------	----------	----------
August 11						
Morning	0.4 (0.8)	0.2 (0.2)	0.2 (0.2)	0.6 (0.4)	0 (-)	0.4 (0.2)
Afternoon	0.2 (0.2)	0.6 (0.2)	0.2 (0.2)	0.8 (0.3)	0.2 (0.2)	0.2 (0.2)
Evening	----------	----------	Rain	----------	----------	----------

Table B4. continued.

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
September 8						
Morning	0.2 (0.2)	0 (-)	0.2 (0.2)	7.2 (2.1)	4.6 (1.2)	2.4 (0.2)
Afternoon	0.8 (0.5)	0.2 (0.2)	0.2 (0.2)	12.4 (2.5)	6.0 (1.6)	3.4 (1.4)
Evening	0 (-)	0.4 (0.3)	0 (-)	5.4 (8.3)	2.4 (2.3)	1.2 (3.2)
September 15						
Morning	0.4 (0.8)	0.8 (0.7)	0.2 (0.2)	14.8 (1.9)	5.2 (0.9)	3.2 (0.7)
Afternoon	0.4 (0.4)	0.2 (0.2)	0.2 (0.2)	20.6 (4.0)	9.8 (2.5)	8.4 (1.4)
Evening	0.2 (0.2)	0.2 (0.2)	0 (-)	12.4 (52.3)	10 (38.5)	3.4 (7.3)
September 22						
Morning	0 (-)	0.2 (0.2)	0.2 (0.2)	16.6 (2.1)	7.4 (1.1)	6.4 (2.0)
Afternoon	0.2 (0.2)	0.2 (0.2)	0.4 (0.2)	13.0 (1.64)	5.8 (1.6)	4.4 (0.9)
Evening	0.2 (0.2)	0 (-)	0.2 (0.2)	7.6 (7.3)	7.8 (3.7)	1.2 (0.7)

[a]Small = length < 12.5 mm; Medium = length 12.5 mm - 25 mm; Large = length > 25mm

Table B5. Summary of the predator population densities (variance) at Green Acres, 1982. (Mean number/91 cm row)

Date	Total	Clubionidae	Thomisidae	Peucetia viridans (H.)	Salticidae	Oxyopes salticus H.	Small Spiders	Lycosidae	Other Spiders	Formicidae
July 6										
Morning	0.2 (0.2)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Afternoon	1.0 (2.0)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0 (-)	0 (-)	0 (-)
July 13										
Morning	0.4 (0.3)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Afternoon	0.6 (0.8)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 20										
Morning	0.8 (0.3)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0.2 (0.2)	0 (-)	0 (-)	0 (-)
Afternoon	----------				Rain		----------			
July 27										
Morning	4.0 (6.5)	0.4 (0.6)	0 (-)	0.2 (0.2)	0 (-)	0.2 (0.2)	0.4 (0.3)	0 (-)	1.0 (2.0)	0 (-)
Afternoon	4.8 (9.2)	0.2 (0.2)	0.4 (0.3)	0.2 (0.2)	0 (-)	0.8 (0.7)	0 (-)	0.2 (0.2)	0.2 (0.2)	0.2 (0.2)
August 3										
Morning	3.4 (2.3)	0.4 (0.3)	0.6 (0.3)	0 (-)	0 (-)	0 (-)	0.6 (0.3)	0 (-)	0 (-)	0 (-)
Afternoon	2.4 (6.8)	0 (-)	0.2 (0.2)	0 (-)	0 (-)	0 (-)	0.6 (1.8)	0 (-)	0 (-)	0.2 (0.2)

Carabidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus (Reuter)	Reduviidae
0	0	0.2	0	0	0	0	0	0	0
(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)	(-)
0	0	0.6	0	0	0	0	0	0.2	0
(-)	(-)	(0.8)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)
0	0.2	0	0	0.4	0	0	0	0.2	0
(-)	(0.2)	(-)	(-)	(0.3)	(-)	(-)	(-)	(0.2)	(-)
0	0	0.2	0	0	0	0	0	0	0
(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)	(-)
0	0	0.2	0	0.2	0	0	0	0.2	0
(-)	(-)	(0.2)	(-)	(0.2)	(-)	(-)	(-)	(0.2)	(-)
Rain									
0	0	0.8	0	0.6	0.2	0	0	0.2	0
(-)	(-)	(0.7)	(-)	(0.8)	(0.2)	(-)	(-)	(0.2)	(-)
0	0.2	1.2	0	0.6	0.2	0	0.2	0.2	0
(-)	(0.2)	(1.2)	(-)	(0.8)	(0.2)	(-)	(0.2)	(0.2)	(-)
0	0	1.2	0	0.2	0	0	0.2	0.2	0
(-)	(-)	(1.7)	(-)	(0.2)	(-)	(-)	(0.2)	(0.2)	(-)
0	0	1.0	0	0.2	0	0	0.2	0	0
(-)	(-)	(1.5)	(-)	(0.2)	(-)	(-)	(0.2)	(-)	(-)

Table B5. continued.

Date	Total	Clubionidae	Thomisidae	Peucetia viridans (H.)	Salticidae	Oxyopes salticus H.	Small Spiders	Lycosidae	Other Spiders	Formicidae
August 10										
Morning	7.0	0.6	0	0.2	0.2	0.2	0.4	0	0	0
	(12.5)	(0.3)	(-)	(0.2)	(0.2)	(0.2)	(0.3)	(-)	(-)	(-)
Afternoon	3.4	0.2	0	0.2	1.0	0	0	0	0	0
	(4.3)	(0.2)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)
August 17										
Morning	3.4	0.2	0	0	0.4	0	0	0	0	0
	(13.3)	(0.2)	(-)	(-)	(0.3)	(-)	(-)	(-)	(-)	(-)
Afternoon	4.4	0.2	0.2	0.2	0	0	0.2	0	0	0
	(3.8)	(0.2)	(0.2)	(0.2)	(-)	(-)	(0.2)	(-)	(-)	(-)
August 24										
Morning	3.6	0	0	0	0	0	0	0.2	0	0
	(6.8)	(-)	(-)	(-)	(-)	(-)	(-)	(0.2)	(-)	(-)
Afternoon	5.6	0.4	0	0	0	0	0.2	0	0.2	0.6
	(5.8)	(0.3)	(-)	(-)	(-)	(-)	(0.2)	(-)	(0.2)	(1.8)
August 31										
Morning	4.0	0	0	0	0	0	1.2	0	0	0
	(2.0)	(-)	(-)	(-)	(-)	(-)	(0.7)	(-)	(-)	(-)
Afternoon	1.4	0	0.2	0	0	0	0	0	0	0
	(1.3)	(-)	(0.2)	(-)	(-)	(-)	(-)	(-)	(-)	(-)
September 7										
Morning	7.4	0	0	0.2	0.2	0	1.4	0.4	0	0.6
	(28.3)	(-)	(-)	(0.2)	(0.2)	(-)	(2.8)	(0.3)	(-)	(0.8)
Afternoon	5.0	0	0	0	0	0.2	0.4	0	0	0.2
	(9.5)	(-)	(-)	(-)	(-)	(0.2)	(0.3)	(-)	(-)	(0.2)
September 14										
Morning	3.2	0.2	0	0	0.2	0	0.8	0.2	0.2	0
	(2.7)	(0.2)	(-)	(-)	(0.2)	(-)	(1.2)	(0.2)	(0.2)	(-)
Afternoon	3.8	1.0	0	0	0.2	0	1.0	0	0	0
	(2.2)	(-)	(-)	(-)	(0.2)	(-)	(1.5)	(-)	(-)	(-)

Carabidae	Dermaptera	Geocoris spp.	Neuroptera	Notoxus spp.	Orius spp.	Predaceous Pentatomidae	Nabidae	Spanogonicus albofasciatus (Reuter)	Reduviidae
0	0.4	3.8	0	0.2	0	0	1.0	0	0
(-)	(0.3)	(5.2)	(-)	(0.2)	(-)	(-)	(1.5)	(-)	(-)
0	0.2	1.2	0	0	0.2	0	0.2	0.2	0
(-)	(0.2)	(1.7)	(-)	(-)	(0.2)	(-)	(0.2)	(0.2)	(-)
0	0	1.2	0	0	0.2	0	1.2	0.2	0
(-)	(-)	(1.7)	(-)	(-)	(0.2)	(-)	(1.7)	(0.2)	(-)
0	0	2.0	0	1.2	0.2	0	0	0	0
(-)	(-)	(4.0)	(-)	(2.7)	(0.2)	(-)	(-)	(-)	(-)
0	0	1.8	0	0	0	0	1.2	0	0.4
(-)	(-)	(4.2)	(-)	(-)	(-)	(-)	(1.7)	(-)	(0.3)
0.2	0	1.2	0	0.6	0	0	1.0	0.2	0.8
(0.2)	(-)	(1.2)	(-)	(1.8)	(-)	(-)	(2.0)	(0.2)	(1.7)
0	0	1.6	0	0	0	0	1.0	0.2	0
(-)	(-)	(2.3)	(-)	(-)	(-)	(-)	(1.5)	(0.2)	(-)
0	0	0.2	0	0	0	0	0.4	0.2	0.4
(-)	(-)	(0.2)	(-)	(-)	(-)	(-)	(0.3)	(0.2)	(0.3)
0.6	0	1.8	0	0.8	0	0	2.6	0	0.2
(0.8)	(-)	(1.7)	(-)	(1.7)	(-)	(-)	(10.8)	(-)	(0.2)
0.2	0	1.8	0	0	0	0	0.6	0.2	0.8
(0.2)	(-)	(1.7)	(-)	(-)	(-)	(-)	(1.8)	(0.2)	(1.7)
0	0	1.0	0	0.2	0	0	0.2	0.2	0
(-)	(-)	(1.0)	(-)	(0.2)	(-)	(-)	(0.2)	(0.2)	(-)
0	0	1.2	0	0	0	0	0.2	0	0.2
(-)	(-)	(1.7)	(-)	(-)	(-)	(-)	(0.2)	(-)	(0.2)

Table B6. Summary of the density of populations of other lepidopterous larvae and velvetbean caterpillar larvae (variance) at Green Acres, 1982. (Mean number/91 cm row)

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
July 6						
Morning	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Afternoon	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 13						
Morning	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Afternoon	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
July 20						
Morning	0 (-)	0 (-)	0 (-)	0.4 (0.3)	0 (-)	0 (-)
Afternoon	----------	----------	Rain	----------	----------	----------
July 27						
Morning	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
Afternoon	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)

Table B6. continued.

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
August 3						
Morning	0 (-)	0 (-)	0 (-)	1.2 (1.2)	0.2 (0.2)	0 (-)
Afternoon	0.6 (0.8)	0 (-)	0 (-)	1.8 (3.2)	0.6 (0.8)	0.4 (0.8)
August 10						
Morning	0.4 (0.3)	0 (-)	0 (-)	4.2 (0.7)	2.2 (4.2)	0 (-)
Afternoon	0 (-)	0.2 (0.2)	0 (-)	3.0 (2.5)	1.4 (4.3)	0.8 (1.2)
August 17						
Morning	0 (-)	0 (-)	0.2 (0.2)	2.6 (7.3)	4.4 (4.3)	1.0 (1.5)
Afternoon	0.2 (0.2)	0 (-)	0.4 (0.3)	2.8 (2.7)	2.8 (2.7)	0.8 (1.2)
August 24						
Morning	0.4 (0.3)	0 (-)	0.2 (0.2)	9.2 (24.7)	8.0 (22.0)	2.4 (2.3)
Afternoon	0.4 (0.3)	0.2 (0.2)	0.8 (0.2)	7.0 (15.5)	3.0 (8.5)	0.6 (0.3)

Table B6. continued.

Date	Other Lepidoptera Larvae			Velvetbean Caterpillar Larvae		
	Small[a]	Medium[a]	Large[a]	Small[a]	Medium[a]	Large[a]
August 31						
Morning	0.4 (0.3)	1.0 (1.0)	0.6 (0.3)	8.6 (18.8)	7.8 (10.7)	1.6 (3.3)
Afternoon	0 (-)	1.8 (2.7)	0.6 (0.8)	11.8 (70.7)	6.0 (6.0)	2.8 (4.2)
September 7						
Morning	0.2 (0.2)	0.2 (0.2)	0.6 (0.3)	18.0 (272.5)	4.2 (4.7)	1.8 (7.2)
Afternoon	0.4 (0.3)	0.8 (1.2)	0.6 (0.3)	10.2 (43.7)	5.2 (3.7)	2.4 (3.3)
September 14						
Morning	0 (-)	0.6 (0.8)	0 (-)	1.4 (1.3)	0 (-)	0 (-)
Afternoon	0.6 (0.8)	0.6 (0.8)	0.2 (0.2)	2.8 (5.2)	0 (-)	0 (-)

[a]Small = Length < 12.5 mm; Medium = length 12.5 mm - 25 mm; Large = length > 25 mm

Table B7. Comparisons of the ratio of alternate prey to velvetbean caterpillar released at Green Acres. The χ^2 for small larvae has 2 degrees of freedom and the χ^2 for medium larvae has 1 degree of freedom.

Week	Small Larvae	Medium Larvae
1	2.09	0
2	0.59	0.01
3	0.008	0.02
4	0.12	0.28
5	0.31	0.91
6	0.02	0.002
7	0.16	0.01
8	0.28	0.07

APPENDIX C
SUMMARY OF LEAF AREA

Table C1. Summary of the leaf area estimates for 1980 and 1982.

Date	1980 (cm2)	1982 (cm^2)
July 6 - 7	4250.12	8700
July 13 - 14	8712.5	10470
July 20 - 21	11772.95	25950
July 27 - 28	17081.48	29685
August 3 - 4	33743.5	54285
August 10 - 11	38585.1	54285
August 17 - 18	27870.36	61395
August 24 - 25	20073.34	76395
September 1 - 7	16783.38	65085
September 14	-	49470

BIOGRAPHICAL SKETCH

Mary Kristine Elvin was born September 22, 1956, in Sheldon, Iowa. After spending her early years in Iowa, she and her family moved to Texas. Kris attended and graduated from Huntsville High School. She enrolled at Texas A&M University, College Station, in 1974 and received a Bachelor of Science degree in entomology in May 1977. Kris continued her education at Iowa State University, Ames, and received a Master of Science degree in entomology in November 1979. She enrolled at the University of Florida, Gainesville, in September 1979. Kris is a member of the Entomological Society of America and the Florida Entomological Society.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Botany

This thesis was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

April, 1983

Dean, College of Agriculture

Dean for Graduate Studies and Research

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